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Bulletin

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BULLETIN OF THE TORREY BOTANICAL CLUB
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THE SHOOT APICES OF ATHROTAXIS AND TAIWANIA[1]

G. L. CROSS

INTRODUCTION

It has been demonstrated that the apical meristem in seed plants does not consist of a homogeneous aggregation of cells, but that it is differentiated into "growth zones" which may be distinguished from each other by differences in cellular size, rate and plane of cellular division, staining reaction, vacuolation, thickness of cell walls and polarity of growth (Foster 1941). The structural and functional relationships of the growth zones in species from several major groups of plants, ranging from the Lycopodiales to the Monocotyledons, have been studied recently, and considerable variation has been reported. Although the various species in a family may possess shoot apices with similar fundamental features of cellular organization, these features are not always found in the species of other, apparently related families and, therefore, homology or equivalence of growth zones in the various groups is difficult to determine (Foster 1939a). Further, many perplexing and seemingly inconsistent differences of detail are sometimes found when the apices of the various species of a genus are compared carefully (Cross 1938, Foster 1939a, Cross and Johnson 1941). And finally, although the structural features of the shoot apices of individuals belonging to the same species are reasonably constant, variation in cellular pattern is often found, and there is good evidence that even a single apex may change markedly during the seasonal development of a shoot (Cross 1943) or in relation to the initiation of foliar primordia (Cross and Johnson 1941, Reeve 1942). The evolution of the apical meristem in the various groups is a puzzling problem which can be solved only when considerable additional information is available.

It seems evident that one step toward the solution of the problem must be the acquisition of information concerning the shoot apices of a considerable number of *species* of plants; i.e., specific information concerning: (1) the fundamental structural features which are characteristic of the apices of representative species belonging to the same taxonomic group; (2) the changes of cellular pattern which occur in the apices of individual plants during a growing season; and (3) the significance of the changes in cellular pattern with respect to the growth of the shoot as a whole. Only after such a comprehensive, detailed survey of species has been made will it be possible to generalize concerning the relationships of the shoot apices in the major taxonomic units. The information should be useful not only to

[1] Contribution from the Botanical Laboratory of the University of Oklahoma n.s. 79.

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students of phylogeny, but to other investigators as well, for it has been shown that knowledge of the apical meristem can be used with unique effectiveness in studying several phases of shoot morphology (Satina and Blakeslee 1941) and in certain fields of experimental genetics (Cross and Johnson 1941, Cross 1943).

In 1939, the writer began a survey of the shoot apices of species from each genus in the Taxodiaceae, and to date *Taxodium distichum* Rich., *Cryptomeria japonica* (L. F.) Don, *Cunninghamia lanceolata* (Lamb.) Hook., *Sequoia sempervirens* (Lamb.) Endl., and *Sequoiadendron giganteum* (Lindl.) Buch. have been studied. Materials for completing the study of the family are on hand, with the exception of apices of *Glyptostrobus*, and it is hoped that shoot tips of this little-known genus may be obtained from the native habitat in southern China, after the war.

The earlier invesigations (Cross 1939, 1941, 1942, 1943) indicate that, although generic and specific differences do exist, there are basic similarities in form and cellular pattern of the shoot apices which may be used to characterize the family. With respect to form, the apices of the investigated genera vary from hemispherical in *Taxodium* and *Cryptomeria* to conical in *Cunninghamia*. The prevailing cellular pattern differs from those reported recently for other genera of the Coniferales (Korody 1937). In each species of the Taxodiaceae the apical meristem has been found to consist of: (1) a single tier of self-perpetuating apical initials, which may divide periclinally as well as anticlinally; (2) a protoderm in which the cells divide strictly anticlinally except that periclinal divisions may occur rarely in at least one species (Cross 1943); (3) a variable number of subapical mother cells in which divisions occur in diverse planes; (4) a ring or cylinder of peripheral meristem; and (5) a core of pith mother cells. The functional relationships of these "growth zones" are reasonably constant in the various species. The apical initials constitute the source from which the remainder of the shoot apex is derived. Lateral derivatives of the apical initials augment the protoderm and basal derivatives become subapical mother cells. Lateral and basal derivatives of the subapical mother cells contribute to the peripheral meristem and pith mother cells respectively.

The main differences found when apices of the various species are compared involve: (1) the extent to which periclinal divisions occur in the apical initials, and (2) the genetic relationships of the cells of the peripheral meristem and the pith mother cells. In most genera the line of demarcation between the peripheral meristem and the pith mother cells is reasonably sharp, however in certain apices of *Cunninghamia* the distinctions are obscure, and occasionally the cells which occupy the *position* of pith mother cells appear to proliferate laterally toward the peripheral meristem (Cross 1942, fig. 10a). Of course, there are differences in size also; the largest shoot apex (diameter 220 μ) measured thus far was from a strong lateral branch

of *Sequoia sempervirens*, and the smallest (diameter 45 μ) was from a weak lateral branch of *Sequoiadendron giganteum*. All measurements were made in a plane equidistant from the summit of the apex and the axil of the youngest foliar primordium.

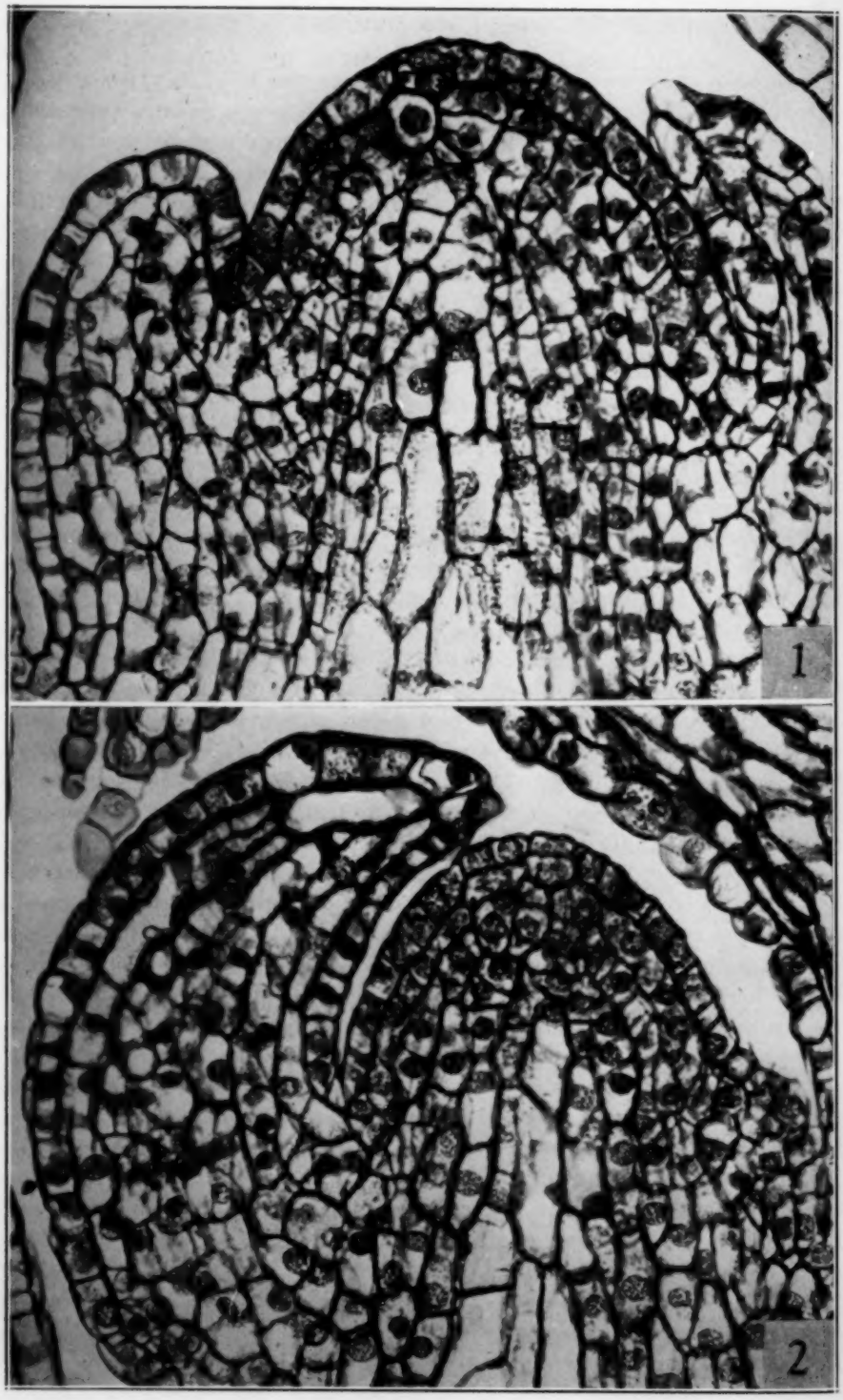
The present study of the shoot apices of *Athrotaxis selaginoides* Don and *Taiwania cryptomerioides* Hayata is confined to a comparison of the fundamental structural features found in these species with the features described previously for other species of the Taxodiaceae. Materials available were limited and it was not thought practicable to attempt a study of seasonal variations in cellular pattern.

METHODS

According to the accounts of Pilger (1926) and Chamberlain (1935), *Athrotaxis* and *Taiwania* are very restricted in natural distribution. *Athrotaxis* apparently occurs only in the mountainous areas of western Tasmania, while *Taiwania* is limited to forested mountains of Formosa and Yünnan. The trees have not been planted extensively in the botanical gardens or parks of the United States and, as might be expected, materials for study were very difficult to obtain.

However, through the kindness of Professor John T. Buchholz, a limited number of shoots of *Athrotaxis* were obtained from a plant—possibly the only living specimen in the United States—growing in a private garden near Golden Gate Park, San Francisco. Professor Buchholz had preserved the branchlets in formalin-acetic-ethyl alcohol. Grateful acknowledgment is made also to Dr. William Hertrich, Curator of the Huntington Botanical Gardens at San Marino, California, who supplied a number of fresh shoots of *Taiwania*. These were fixed by the writer under reduced pressure in a mixture of 5 per cent commercial formalin and 6 per cent glacial acetic acid, made up in 70 per cent ethyl alcohol.

The materials were processed and the illustrations prepared as described in previous papers (Cross 1937, 1939, 1940). Although all of the materials were processed in essentially the same manner, the end results were quite different, especially so with respect to staining reactions. The cytoplasm in the cells of *Athrotaxis* stained very lightly (figs. 1, 2) when safranin and fast green were applied, but in *Taiwania* the cytoplasm stained densely, so much so as to interfere with satisfactory differentiation (figs. 3–6). Perhaps this phenomenon was a result of differences in the degree of activity of the meristem of the two genera, or perhaps killing and fixation may have been less rapid in the larger apices of *Taiwania*. Fixation of the cells of *Athrotaxis* was generally satisfactory, but considerable plasmolysis occurred in those of *Taiwania*. Perhaps the cytoplasm of *Taiwania* stained more densely because the vacuoles had been reduced in size by the plasmolyzing action of the fixing reagents.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GENERAL FEATURES OF THE VEGETATIVE SHOOTS

Both species are trees; according to Pilger (1926), *A. selaginoides* attains a height of 13–15 meters and is strongly branched, while *T. cryptomerioides* may reach 50 meters and is branchless for about one-half of its height.

The vegetative shoots of *Athrotaxis* consist of sturdy, rigid axes upon which the leaves are born in a loose, spiral arrangement which often appears imbricate. The leaves are persistent, leathery, awl-shaped or lanceolate, and keeled on the abaxial surface. According to Pilger (1926) the leaves may grow to a length of 1 cm., but the basal portions (approximately one-half of each leaf) are undiverged from the shoot axis. Bud scales are not found on the vegetative shoots, but the leaves which have formed the outer constituents of dormant buds are usually considerably smaller than the others and, therefore, it is easy to determine the limits of the yearly growth-increments.

The vegetative shoots of *Taiwania* resemble those of *Athrotaxis* in that they consist of rigid stems and spirally arranged leaves. The leaves from the lower portions of a tree or from a young plant (Pilger 1926) are from linear to needle-shaped, very stiff and sharp, laterally flattened, and keeled on both the abaxial and adaxial surfaces. They may be as long as 15 mm., but a broad, basal portion of each leaf is undiverged from the shoot axis. Leaves from the upper portions of a tree are much shorter and scale-like. They are quite thick and appear triangular when viewed from the upper or lower surface. The adaxial keel is usually reduced, and in some instances the upper surfaces of the leaves may be slightly concave, with inwardly turned tips. Bud scales are not found.

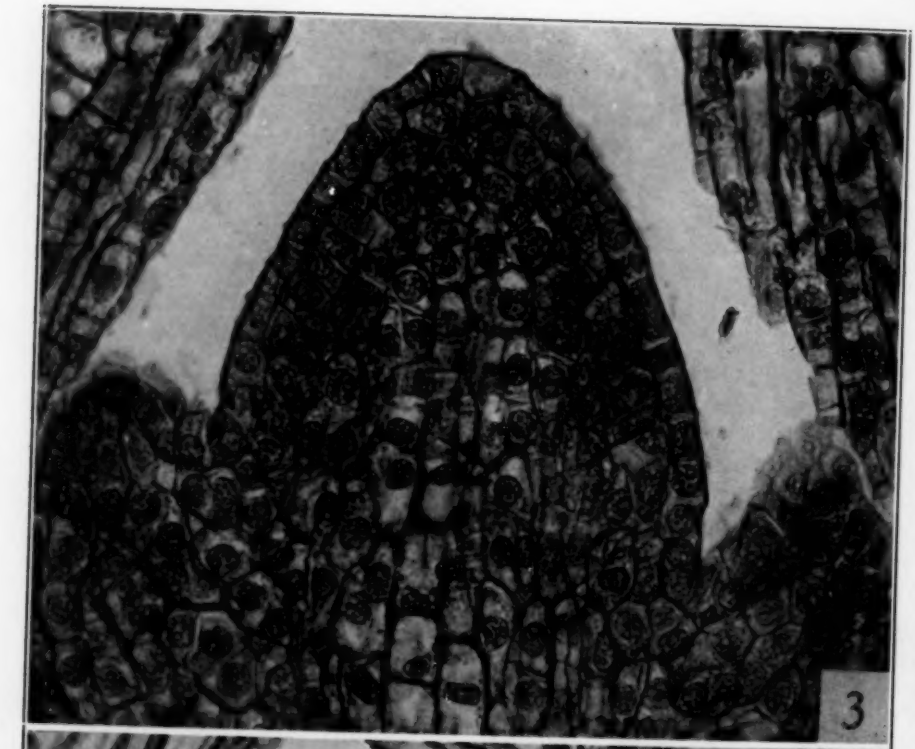
STRUCTURAL FEATURES OF THE SHOOT APICES

Although the literature was searched carefully, no reference to the shoot apices of either *Athrotaxis* or *Taiwania* was found. However, the results of this investigation indicate definitely that the apical meristem in each of these genera is characterized by the same fundamental features of organization that have been described for other representatives of the Taxodiaceae. As a matter of fact, the similarities are so marked that detailed descriptions of the apices of *Athrotaxis* and *Taiwania* will not be necessary—only a brief comparative treatment need be given.

The apices of *Athrotaxis* are hemispherical and, with respect to form, resemble those of *Cryptomeria* (Cross 1941). They vary in diameter from 65 to 120 μ, measured in a plane equidistant from the shoot tip and the axil of the youngest leaf. They rank, therefore, with those of *Cryptomeria* and

Explanation of figures 1, 2.

FIG. 1. Nearly median longisection of shoot apex and foliar primordium of *Athrotaxis*. × 484. FIG. 2. Nearly median longisection of shoot apex and older leaf of *Athrotaxis*. Note continuity of protoderm on flank of apex and over the leaf. × 484.



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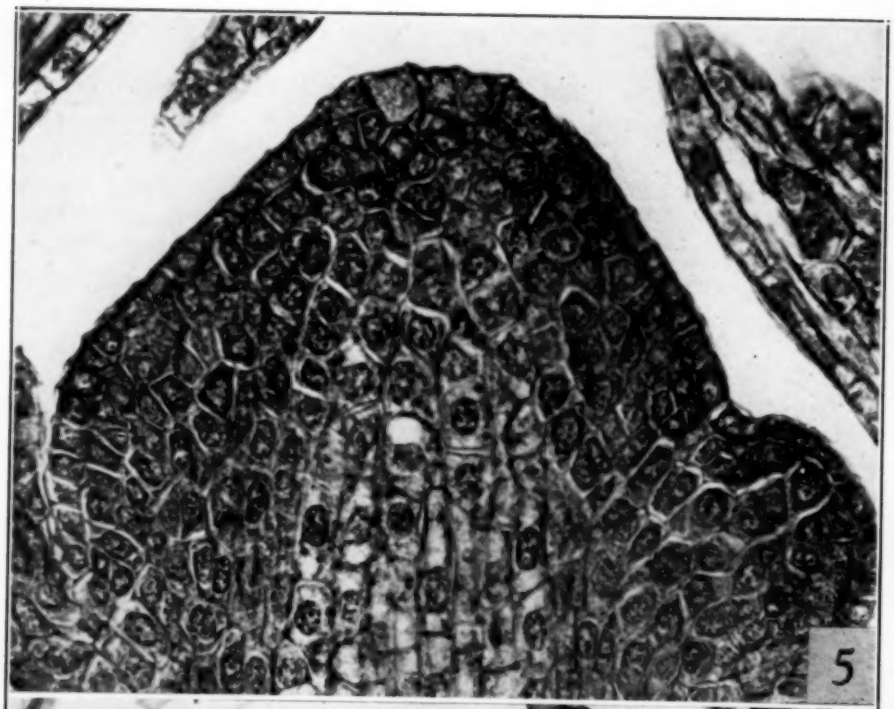
the lateral shoots of *Sequoiadendron* (Cross 1943), among the smallest recorded for the Taxodiaceae. On the other hand, the apices of *Taiwania* are conical and appear parabolic in longisection like those of *Cunninghamia* (Cross 1942). They are somewhat more massive, and a range in diameter of from 90 to 160 μ was found in the twenty-five shoot tips which were measured. An idea of the variation in size and form may be obtained from a careful comparison of figures 1–6. The structural features of the apices of the two genera are discussed in the following paragraphs.

The Apical Initials. The summit of the apical meristem consists of a single tier of self-perpetuating apical initials which divide periclinally as well as anticlinally and, although 25 apices of each species were examined, no indication of a discrete surface layer over the tip of the apical meristem was found (figs. 1, 2, 3–6). Apparently the periclinal and anticlinal divisions occur with approximately equal frequencies, and in this respect the apices of *Athrotaxis* and *Taiwania* resemble those of *Cunninghamia* (Cross 1942). Occasionally an oblique division may produce a triangular apical cell (fig. 4) suggestive of those found regularly in the shoot tips of many species of leptosporangiate ferns. Doubtless Korschelt's (1884) report of an apical cell in the shoot tips of *Taxodium* was based upon studies of sections similar to the one represented by figure 4. However, it seems evident that this phenomenon occurs infrequently, and the cellular pattern which results is transitory. As in other species of the Taxodiaceae, but unlike those of the Abietaceae, lateral derivatives of the apical initials differentiate into a protoderm; the basal derivatives become subapical mother cells.

The Protoderm. The presence of a protoderm on the flanks and lower shoulders of the apical meristem has been demonstrated for each of the investigated species of Taxodiaceae. In this layer mitotic figures are almost always oriented parallel with the surface of the meristem, and in the apices of *Athrotaxis* and *Taiwania* the resulting uniseriate layer is clearly delimited from the underlying tissue by a thicker, more heavily staining wall which can be traced down the flanks of the apical meristem and over the tips of the foliar primordia. This feature is usually conspicuous in the apices of *Athrotaxis* (figs. 1, 2), but it may be observed without difficulty in those of *Taiwania* (figs. 3–6). Periclinal divisions in the protoderm have been reported to occur rarely in *Sequoia sempervirens* (Cross 1943) and in *Sciadopitys* (Strasburger 1872) on the flanks of the apical meristem, but they have not been reported to occur during foliar initiation in any species of the

Explanation of figures 3, 4.

FIG. 3. Nearly median longisection of apex of a smaller lateral shoot of *Taiwania*. Note sequence of walls in the apical initials. × 484. FIG. 4. Nearly median longisection of apex of a more vigorous shoot of *Taiwania*. Note triangular "apical cell" at the summit. × 484.



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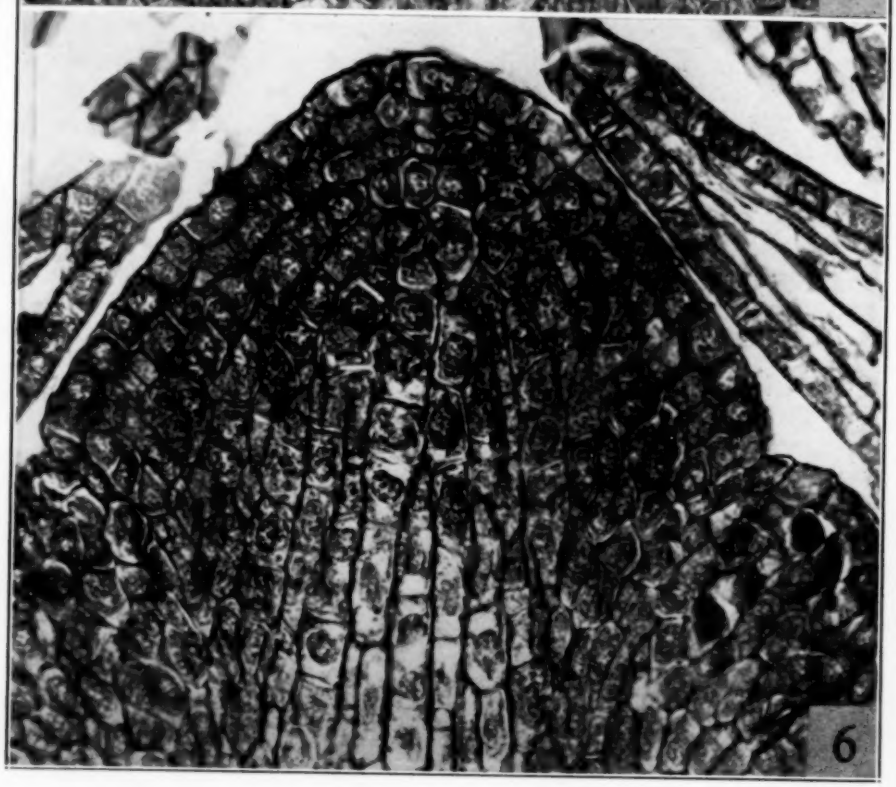

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Taxodiaceae. In this respect the apices of the Taxodiaceae contrast sharply with those of the Abietaceae (Korody 1937) but are comparable with those of *Araucaria* and *Ephedra* (Strasburger 1872).

The Subapical Mother Cells. Subapical mother cells, arising from the inner derivatives of the subapical initials, are of common occurrence in the Gymnosperms. They exist, at least theoretically in all species which have periclinally dividing apical initials, although their delimitation from other subterminal growth zones (peripheral meristem and pith mother cells) may not always be well marked. In *Athrotaxis* and *Taiwania*, as in other genera, they are distinguished by their position, their diversity with respect to planes of cellular division, and to a lesser extent by their inconspicuous vacuolation. Considerable quantitative variation is noticed when individual apices are studied. Thus in figure 1 the zone of subapical mother cells is limited vertically, and the pith mother cells extend to within a very few cell layers of the summit of the axis. In figure 2 this zone has a greater vertical extension, and the pith mother cells are differentiated much lower in the shoot tip. The reasons for these variations are not understood.

During the investigation it was noticed that the nuclei in the shoot apices of *Athrotaxis* appear to be smaller than those of *Taiwania*, although similar differences in cellular size were not so apparent. Twenty-five nuclei from each genus were measured, using a camera lucida and a card ruler drawn to the proper scale, and it was found that the nuclei of *Athrotaxis* are from 6 to 7 μ in diameter, whereas those of *Taiwania* are from 9 to 10 μ. An equal number (25) of major and minor cellular dimensions were also determined for the subapical mother cells of each genus. The cells of *Athrotaxis* averaged approximately 9×15 μ, those of *Taiwania* 10×15 μ. While these measurements are only approximations, they give evidence that the ratio of the nuclear volume to cellular volume is somewhat less in *Athrotaxis* than in *Taiwania*. The photomicrographs also provide evidence for this suggestion. A careful statistical study of these features, made by someone to whom adequate cytological materials are available. might be worthwhile.

Lateral derivatives of the subapical mother cells produce the peripheral meristem, while basal derivatives differentiate into pith mother cells.

The Peripheral Meristem. The peripheral meristem is arranged in the form of a ring or cylinder which surrounds the pith mother cells. The limits between this zone and the subapical mother cells is often vague, especially in the smaller apices (figs. 2, 3); however, the cellular divisions in the peripheral meristem are prevailingly anticlinal, and therefore the derivatives

Explanation of figures 5, 6.

Nearly median longisections of the apices of vigorously growing shoots of *Taiwania*. ×484.

are arranged in strata. The number of layers varied from two to three in *Athrotaxis* and from two to four in *Taiwania*. No unusual developmental features were observed. Derivaties of the peripheral meristem become vascular tissue, cortical tissue, and the internal portions of leaves.

The Pith Mother Cells. The pith mother cells are distinguishable at a variable distance (from 3 to 5 cell layers) below the summit of the axis. In *Athrotaxis* they divide once or twice, preponderately in transverse planes, thus forming short vertical files of two or three cells. These cells then gradually enlarge and mature into pith (figs. 1, 2). In *Taiwania* the behavior is similar, although here the files of cells derived from the pith mother cells are sometimes longer, occasionally consisting of four or five cells (figs. 4–6). Enlargement and maturation of these derivatives into pith proceeds at a slower rate than in *Athrotaxis*, therefore mature pith is usually found at a considerably greater distance from the shoot tip. Thus, as in other genera of the Taxodiaceae, an extensive rib meristem is not formed. This is a second feature which contrasts with the situation reported for certain genera of the Abietaceae (Korody 1937), *Zamia* (Johnson 1939), *Cycas* and *Dioon* (Foster 1941) and *Ginkgo* (Foster 1938).

DISCUSSION

The shoot apices of representative species of all genera of the Taxodiaceae except *Sciadopitys* and *Glyptostrobus* have been examined during the past three years. In a recent paper (Cross 1943) it has been suggested that there are basic structural features which characterize the family, because in all investigated species the apical meristem consists of apical initials, a protoderm, subapical mother cells, peripheral meristem, and pith mother cells. The data obtained from the apices of *Athrotaxis* and *Taiwania* support this tentative conclusion.

Self-perpetuating apical initials occur (at least theoretically) in all shoot apices. In the more "primitive" groups, such as the Lycopodiales, Cycadales, and Abietaceae, these initials may divide anticlinally, periclinally or obliquely (Härtel 1938, Foster 1941, Korody 1937). In the more "advanced" groups (Angiosperms) only anticlinal divisions occur in the majority of cases, although Sharman (1940) has shown that exceptions may occur. In the Taxodiaceae the apices of several genera (*Taxodium, Cryptomeria,* and *Sequoia*) show evidence of a reduction in the relative number of periclinal and oblique divisions that occur. Whether this indicates an evolutionary trend toward the development of a discrete surface layer (tunica) in the family remains to be seen.

The occurrence of a protoderm appears to be a relatively "advanced" characteristic, although it is not unique among gymnospermous genera.

This feature does not appear in the apices of the investigated species of *Lycopodium* (Härtel 1938), the Cycadales (Foster 1941, 1943), and the Abietaceae (Strasburger 1872, Korody 1937), although it has been reported in species of *Araucaria* (Strasburger 1872) and *Ephedra* (Strasburger 1872, Gifford 1943). In the Angiosperms a protoderm occurs prevailingly, although in some monocotyledons this layer has the unique feature of dividing periclinally during foliar initiation, and thereby contributes substantially to the internal portions of the foliage leaves (Rösler 1928, Kliem 1937). The fact that the surface layer of the shoot apices of the Taxodiaceae consists of a protoderm on the flanks, and diversely dividing apical initials at the summit, would indicate that this family represents a condition phylogenetically intermediate between the groups which lack a protoderm (Lycopodiales, Cycadales, and Abietaceae) and those which have an entirely discrete surface layer (most Angiosperms). Of course, this does not mean that the family is to be regarded as a "connecting link" between the Gymnosperms and Angiosperms, for admittedly the phylogenetic relationships of these two groups are still obscure. But it may mean that, with respect to shoot apices, parallel evolutionary processes are occurring.

Any shoot apex in which the apical initials divide periclinally may be interpreted as possessing subapical mother cells, a situation which occurs widely in the Gymnosperms. The characteristics of the subapical mother cells vary markedly when apices of various species are compared or even when apices of the same individual are studied; however, these variations are usually of a quantitative nature. The situation is exceedingly complex in some of the Cycads, especially in *Microcycas* (Foster 1943). Here the derivatives of the surface initials are arranged in long files of cells, a portion of which differentiates into peripheral meristem and the remainder into deeply located "central mother cells." The significance of the specialized subterminal region of the apical meristem of cycads to the evolution of shoot apices in seed plants is one of the most puzzling problems associated with shoot histogenesis. It has been suggested that a clue to the answer may be obtained by comparing the cellular patterns found in some of the more "primitive" apices of the Taxodiaceae, such as *Cunninghamia* (Cross 1942) with those of cycad seedlings (Foster 1939b), although much additional work must be done before conclusive results can be obtained. Perhaps a knowledge of the apices of some of the Angiosperms with growth habits similar to those of the cycads would be of aid. In this connection Boke (1941) and Ball (1941) have made recent contributions concerning cacti and palms respectively.

If periclinal divisions do not occur in the apical initials, as is the case in most Angiosperms, the subjacent tier of cells may be regarded as *subapical initials* because, under such circumstances they would be self-perpetuating. Aside from phylogenetic considerations, the occurrence of subapical initials

is of considerable importance to experimental geneticists, especially those working on problems involving polyploidy (Satina and Blakeslee 1941).

A peripheral meristem is found in the apices of all plants in which medullation occurs at a higher level in the axis than the differentiation of cortical parenchyma. This growth zone occurs commonly in Gymnosperms and has been reported for certain species of small-leaved dicotyledons, including certain cacti (Boke 1941) and *Linum* (Esau 1942). In most Gymnosperms and dicotyledons, derivatives of this zone produce foliar primordia (the internal portions), cortical tissue, and provascular tissue.

Pith mother cells, of course, are found in all vascular plants in which a pith occurs. They arise from initiating regions immediately above in the axis (subapical mother cells or subapical initials). The pith mother cells usually develop into a rib meristem which may extend vertically for a considerable distance as in *Ginkgo*, various cycads, and some conifers (Foster 1938, 1941, Korody 1937) or may be very short as in the Taxodiaceae and some Angiosperms (Esau 1942).

From the above discussion it is clear that the structural features found in the shoot apices of the Taxodiaceae are widely distributed among vascular plants. The chief interest of the family lies in the fact that here the various features may be found combined in a single apex. The most unique single characteristic appears to be that the surface layer consists of cells which divide diversely at the summit (apical initials) and only anticlinally (with rare exceptions) on the lower shoulders and flanks. However, Sharman's (1940) report of a periclinally dividing cell in the surface layer at the summit of the apical meristem of *Zea* minimizes the uniqueness of this feature and emphasizes that differences in cellular patterns are often essentially quantitative, i.e., contingent upon the *frequency* with which deviations from the expected behavior inevitably occur. Thus the shoot apices of the Taxodiaceae differ from those of Angiosperms with respect to only one essential feature, viz., the frequency (greater) with which periclinal divisions occur in the surface layer at the summit. They differ from the apices of the Abietaceae only with respect to the frequency (lesser) with which periclinal divisions occur in the surface layer on the flanks of the meristem, and the extent (lesser) to which divisions occur in the rib meristem. Thus, from a phylogenetic point of view, the "transitional" nature of the apical meristem of the Taxodiaceae seems well established.

SUMMARY

The shoot apices of *Athrotaxis* are hemispherical and, in longisection, resemble those of *Cryptomeria*. They are among the smallest reported for the Taxodiaceae, ranging from 65 to 120 μ in diameter in a plane equidistant from the shoot tip and the axil of the youngest leaf. The apices of *Taiwania*

are conical, 90 to 160 μ in diameter, and reminiscent of those of *Cunninghamia*.

The cellular patterns in each genus resemble those of the previously investigated genera of the Taxodiaceae, and no unusual features were observed. The apical meristem consists of a single tier of self-perpetuating *apical initials;* a *protoderm*, derived from lateral derivatives of the apical initials; *subapical mother cells*, derived from basal derivatives of the apical initials; *peripheral meristem*, derived from lateral derivatives of the subapical mother cells; and *pith mother cells*, derived from basal derivatives of the subapical mother cells. The subterminal growth zones (subapical mother cells, peripheral meristem, and pith mother cells) are rather poorly delimited, especially in the smaller apices of each genus.

With respect to the structural features of the surface layer of the apical meristem, the genera of the Taxodiaceae are regarded as intermediate between the more primitive Gymnosperms (Cycadales and Abietaceae) and the Angiosperms, although this is probably to be regarded as a case of parallel evolution rather than phylogenetic relationship.

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Norman, Oklahoma

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THE MORPHOLOGY AND ANATOMY OF CALOPOGON PULCHELLUS

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Orchids, particularly the tropical species, have been studied by numerous investigators, especially with regard to the breeding of new varieties, the germination of the seeds, and the relationship to mycorrhizal fungi, but in spite of the importance of their morphology in determining their relationship with other seed plants, much work remains to be done.

Beginning with the investigations of the morphology of orchids by Irmisch (13) in 1853, many pieces of work have treated the subject of the anatomy of the several organs of orchid plants. These investigations are listed in the chronological bibliography presented by Solereder and Meyer (17). The observations were collected and extended by them in their chapter on the Orchidaceae, from which one can obtain specific information about the cell structure, cell contents, and arrangement of cells in leaves, stems, and roots of mature plants of hundreds of species of orchids.

Probably the earliest attempt to treat the anatomy of the monocotyledons comparatively was that of Guillaud (12) in 1878. He presented a brief life history of *Epipactis palustris* Crantz. as representative of the orchids. Some attention was paid to the orchids by de Bary (2) in his "Comparative Anatomy," but perhaps the best known work in this field is that of Arber (1). She summarized the available information on the development and structure of the orchids with a view to showing their relationship to the other monocotyledons. She pointed out the importance of using knowledge of internal structure as well as knowledge of external form in the study of phylogeny, and emphasized the inadequacy of our knowledge of the anatomy of the orchids.

Recently Fuchs and Ziegenspeck (8, 9, 10) made an extensive study of the structure and development of terrestrial orchids native to Europe. Because they were unsuccessful in growing plants from seed, they collected their plants in various stages of development in the field. They described and diagramed the gross anatomy and developmental story, studied cross and longitudinal sections to determine the character and arrangement of the tissues, and traced the entrance and penetration of the mycorrhizal fungi. They studied plants belonging to the following genera: *Orchis, Cypripedium, Helleborine, Limodorum, Cephalanthera, Listera, Neottia, Goodyera,*

[1] The author wishes to express her thanks to the Boyce Thompson Institute for Plant Research for the use of its facilities while this work was in progress and for furnishing the photomicrographs.

Liparis, Achroanthus, Malaxis, Corallorhiza, Epipogon, Spiranthes, Coeloglossum, Platanthera, Herminium, Gymnadinea, Nigritella, Neottianthe, and *Ophrys.*

Results of studies on the artificial culturing of orchids may be found in the work of Knudson (14, 15), Curtis (7), and Carlson (5). The recent work of Burgeff (3, 4) summarizes our knowledge of the germination of orchids seeds, the development of seedlings, and the cytology, physiology, and classification of the mycorrhizal fungi and their function in the orchid plants. It gives directions for isolating and identifying the fungi, and for planting seeds and caring for the seedlings, and it contains a good bibliography of these phases of the investigations.

MATERIALS

Calopogon pulchellus (Sw.) R. Br., the grass pink, was chosen for this study because the early stages in its development can be obtained by germinating the seeds and because it has not been studied previously. The species grows in bogs and wet meadows throughout the United States and Canada. Seeds and plants for this study were collected from sphagnum bogs near Sayner, Wisconsin.

The seeds were planted on a nutrient medium in culture bottles, as described by Knudson (14, 15), Curtis (7), and Carlson (5). Seedlings in different stages of development and also parts of older plants collected in the field were fixed in a modified solution of formalin-aceto-alcohol, consisting of 6 parts of 50 per cent alcohol, 3 parts glacial acetic acid and 1 part of formalin. Sections were cut 10 or 12 μ in thickness, mounted in serial order, and stained with safranin and fast green. Great difficulty was encountered in cutting corms whose cells were filled with starch. Fresh corms were sectioned free-hand and the sections kept in serial order on the slides. In most cases the starch was removed with a dilute solution of sulphuric acid and the sections were then preserved on the slide in a 50 per cent solution of glycerine in water.

OBSERVATIONS

The Seed. The seed (fig. 1a) consists of a transparent, loose-fitting seed coat and an ellipsoidal embryo. The seed averages 0.68 mm. in length and 0.20 mm. in width, and the embryo averages 0.27 mm. in length and 0.15 mm. in width (averages from measurements of 60 seeds). The seed coat is a membranous air-filled sac, open at the funicular end where it was broken away from the placenta. It consists of a single layer of elongated, empty cells whose thickened walls give positive tests for lignin and cellulose with the standard methods. The embryo is a mass of undifferentiated parenchymatous cells. The cells in the anterior part (toward the chalazal end of the seed) are small, with dense cytoplasm and centrally placed nuclei, whereas

those of the posterior part are larger and more vacuolated. The embryo is not differentiated into epicotyl, hypocotyl, and cotyledon, but the anterior part of the embryo becomes a bud and might be considered an epicotyl. The much larger posterior portion of the embryo is a food-storage region which might be considered a cotyledon. No primary root is present. Oil globules are found in the dormant embryo, but neither starch nor sugar is present. The walls of the cells of the embryo give a positive test for cellulose. The remains of the integuments and nucellus of the ovule form a brown beak-like cap over the basal, or micropylar, end of the embryo. Filamentous strands of

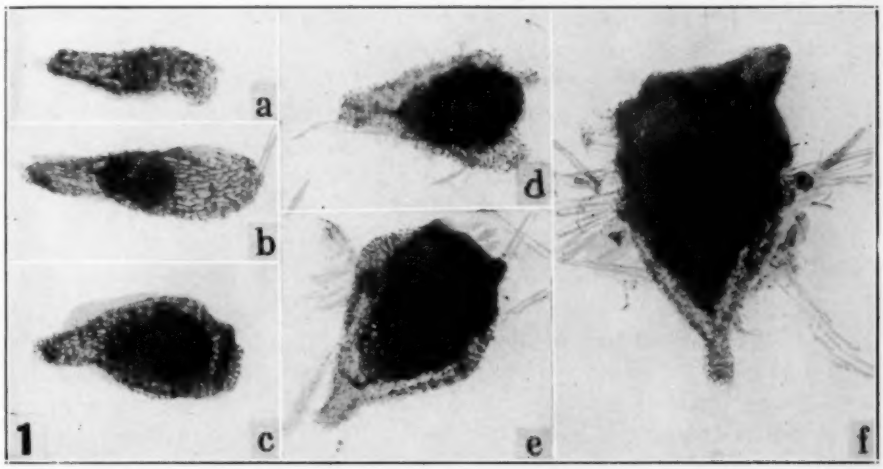


FIG. 1. Seed and young seedlings of *Calopogon pulchellus* (Sw.) R. Br. a. Seed. b. Germinating seed, embryo enlarged. c. Later stage, apical end of embryo becomes a protocorm. d. Protocorm still larger, seed coat split at chalazal end. e. Seedling with protocorm and bud at apical end, primordium of first leaf evident. f. Older seedling showing protocorm, absorbing hairs, developing bud, primordia of two leaves, seed coat still attached.

cells, probably remaining after the disintegration of the inner cells of the ovule, as in *Cypripedium parviflorum* (6), suspend the embryo in the center of the seed coat, and can be seen attached to the embryo when it is removed from the seed coat.

The Seedling. The seeds germinate soon after being planted in a suitable medium (4). The embryo enlarges and becomes green. At first the seedling retains its oval shape (fig. 1b) because the enlargement is uniform in all dimensions, but in a few weeks the apical end enlarges more rapidly than the basal end, both in length and in width, and the seedling becomes egg-shaped (fig. 1c). It stretches the seed coat laterally, and finally splits it at the chalazal end (fig. 1d).

As growth continues, the differences between the apical and basal ends of the seedling become more marked. The cells of the basal part enlarge greatly, whereas those of the upper part divide and produce a typical promeristem. The oil disappears and reducing sugars and starch appear. Certain cells of the epidermis elongate outward and become absorbing hairs which resemble root hairs. These hairs are produced singly or in small groups, and their length depends on external conditions. The seed coat may remain attached for a time, but is eventually shed. The seedling at this stage of development will be called a protocorm, or first corm (fig. 1e).

A bud now develops from the promeristem and appears as a cone-shaped protrusion. A circular ridge of cells, which arises from the promeristem, is the primordium of the first leaf. A second leaf-primordium arises in the same manner, within and above the first (fig. 1f). A median longitudinal section of a seedling at about this stage of development (fig. 4) shows the bud, with its two concentric tubular leaf-primordia enclosing the promeristem, and its food-storage region still constituting the greater part of the seedling.

When mature, the first or outer leaf is only about 2 or 3 mm. long, and consists of a tubular sheath whose tip is somewhat spread out (fig. 2A). The second leaf becomes longer than the first, and extends through and beyond the opening in the tip of the first. The second leaf also has a tubular sheath whose upper part flattens out into a small blade. The second leaf may be from 5 to 10 mm. long when mature (fig. 2B). During the elongation of the first two leaves, a third leaf-primordium develops from the promeristem directly above the second leaf (fig. 5) and a fourth develops above the third. Each new leaf has a sheath-like base which extends through and beyond the opening in the sheath of the preceding leaf. The tip of the sheath becomes an increasingly longer blade on each succeeding leaf (fig. 2E). Usually only four leaves develop on a seedling. They are arranged alternately in two ranks and are attached close together because the internodes do not elongate. The protocorm, that is, the portion of the seedling below the first leaf, may elongate considerably (fig. 2C, D, E).

The first root of the seedling arises adventitiously either in the upper part of the protocorm or in the bud. Its origin and development will be described later.

By mid-season of the first year, the young plant consists of the protocorm with its absorbing hairs, the shoot with its four concentric leaves in two opposite ranks, and usually, although not always, an adventitious root. The first leaf is chiefly a sheath, but the later ones have linear grass-like blades in addition to their sheaths (fig. 2).

During the later part of the first season, the meristematic tip of the stem stops growing, and a new corm (the second) begins to form by the elongation and enlargement of the parenchymatous cells of the two upper internodes of

the stem (figs. 2C, D, E, 6). This increase in diameter of the stem starts abruptly just above the second node (counting from the base upward) and ends abruptly at the fourth node. The first or lowermost internode may also elongate, but it does not enlarge in diameter. If it elongates, it appears as a stalk of variable length between the protocorm and the new corm, and is ensheathed by the first leaf. If it does not elongate, the first two leaves are close together at the base of the corm, and their sheaths are stretched and sometimes split by the enlargement of the corm. Because the new corm con-

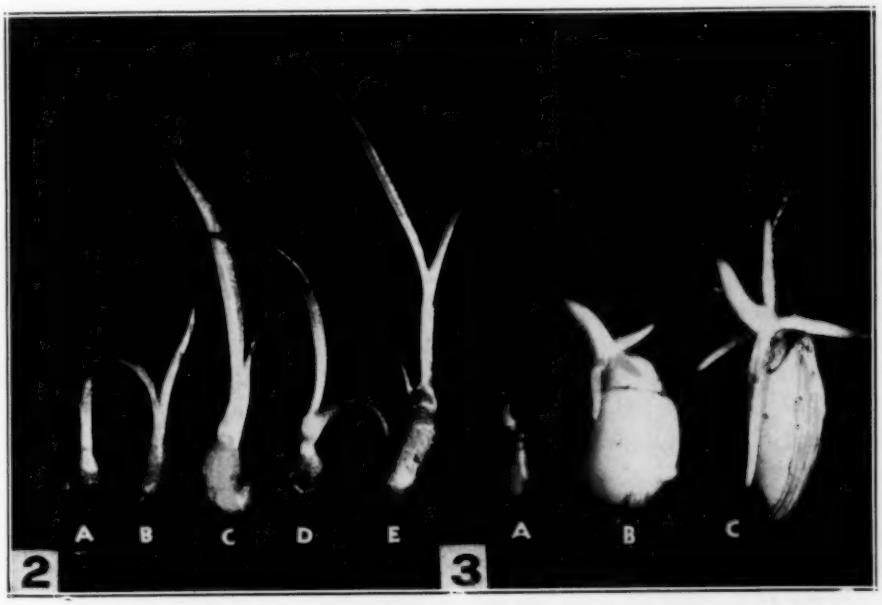


FIG. 2. Plants of first season. A. Young plant with protocorm and young shoot. B. older plant with two leaves expanded. C. Second corm forming at top of protocorm, within sheaths of leaves. D and E. Second corm larger, leaves fully expanded. FIG. 3. Corms of older plants. A. Corm with shoot developing from upper bud, two adventitious roots protruding from base of shoot, lower bud of corm dormant. B. Older corm with developing shoot, whorl of adventitious roots, and dormant lower bud; line across upper part of corm is place of attachment of principal leaf. C. Still older corm with larger shoot and whorl of 7 roots.

sists of the second and third internodes with the intervening third node, the third leaf is attached to the corm. Its base encircles the corm obliquely, usually a little above the middle, and is, of course, much broader than the base of any of the other leaves. Its sheath fits tightly over the top of the corm and encloses the fourth leaf which is attached at the top of the corm. The extreme tip of the corm, which is the meristem of the stem tip, usually dies and appears as a brown spot inside of the sheath of the fourth leaf.

The reserve starch in the cells of the protocorm is gradually digested and passes into the new corm, leaving the protocorm shriveled. The new corm becomes much larger than the protocorm, probably because some of the food manufactured by the leaves and by the corm itself (because its outer layers contain chloroplasts) as well as the excess food from the protocorm passes into the new corm.

The junction between the first and the second corms is seen in figure 6. The first internode has remained short in this case, and the encircling sheaths of the first two leaves are spread apart by the enlarging corm. Because of the abrupt increase in diameter of the second internode, the old and new corms seem to be connected by a narrow neck. Vascular bundles pass from the old to the new corm through this junction, and the cells which surround the bundles in this region become thick-walled and remain free of starch.

As the new corm grows, buds are formed in the axils of the second and third leaves opposite their midribs, but none were found in the axils of the first and fourth leaves. A bud starts as a group of meristematic cells under the epidermis of the corm, and primordia of four leaves develop later from these meristematic cells in acropetal order (fig. 9). The buds develop until they protrude from the surface of the corm, the upper protruding more than the lower. The buds are raised some distance above the attachments of their subtending leaves because the corm enlarges and elongates simultaneously with bud development. A primordium of an adventitious root is formed in each bud. This will be described later.

Toward the end of the first growing season the young plant (fig. 2C, D, E) consists of the small shriveling protocorm which still retains its absorbing hairs; a shoot with four concentric leaves, of which only the upper ones have linear flattened blades; usually an adventitious root arising either from the protocorm or from the base of the shoot; and a second corm filled with starch and enclosed by the sheaths of the leaves.

With the approach of winter, the blades of the leaves succumb to the cold and disintegrate, but their sheaths dry and remain as brown scale-like coverings over the second corm. When all of the food has passed out of the first corm, it gradually disintegrates. The root also dies. Finally all that remains through the winter is the dormant second corm, enclosed by dried sheaths of leaves, with its dormant buds which contain the primordia of leaves and adventitious roots for the next season.

The Plant in the Second Year. With the resumption of growing conditions, the upper lateral bud of the corm begins to grow into a new plant, development, therefore, being sympodial. It breaks through the dried leaf-bases which ensheath the corm. The primordia of the leaves elongate rapidly, but the stem grows rather slowly. The outer leaf becomes a conical sheath

which completely covers the young shoot and gives it the appearance of the seedling shoot of corn. Three or four leaves develop from the bud, of which two have tubular sheaths open at their tops, and the others have linear blades above their sheaths. Each successive leaf is longer than that which precedes it, except the fourth which often does not elongate very much. All of the leaves of the plant of the second year become longer and wider than those of the plant of the first year. The lower bud of the corm, which has the same origin and structure as the upper bud, remains dormant unless the upper bud is removed or injured. The root-tip, which lay dormant in the stem of the bud, elongates and pushes horizontally through the sheath of the first (outermost) leaf of the shoot, and then turns downward.

After the third leaf has completely expanded, another corm (the third) begins to develop in the same manner in which the previous one developed; i.e., by the enlargement and elongation of the second and third internodes of the stem and by the entrance of food from the previous corm. The meristematic tip of the shoot stops growing when the corm begins to form and usually dies. The first (lowermost) internode of the shoot may elongate, but it does not increase in diameter, nor become a part of the new corm. It merely lifts the new corm higher in the medium in which the plant is growing. As in the plant of the first year, buds are differentiated in the axils of the second and third leaves, and a root primordium appears in each bud.

At the end of the second growing season, the plant is larger than, but otherwise similar to, the plant of the first season. It consists of the wrinkled second corm, a lateral shoot with three leaves, a single root, and the third corm enclosed by the sheaths of the leaves. The internode separating the corms may or may not elongate. The tip of the stem dies and appears as a brown spot terminating the corm. Finally all of the plant except the upper corm dies, and the old corm and root disintegrate. The upper corm, enclosed by the dry, brown leaf-bases, lies dormant until the next spring.

Older Plants. The exact age of plants older than two years could not be determined because they were collected in the field and not grown from seeds. However, it was assumed that the larger the corm, the older the plant. A series of increasingly larger corms was studied. The history of their development in succeeding years was found to be much the same as in the first two years.

Each year the plant becomes increasingly larger and more complex (fig. 3A, B, C). Each year a lateral shoot develops sympodially from the upper bud of the dormant corm. If, however, the upper bud is injured, a shoot develops from the lower bud. The shoot produces a short stem, and from three to five concentric leaves. The first two or three leaves are entirely sheathing; the third or fourth bears a lanceolate blade; and the fourth or fifth may or

may not elongate. Each year until the plant is mature, the blade of the principal leaf becomes longer and wider. Each year an increasing number of adventitious roots appears at the base of the shoot. Each year, after the leaves and roots are fully developed, a new corm is formed by the enlargement of the two upper internodes of the stem, and this corm may be lifted upward by the elongation of the first internode of the shoot. A bud is formed in the axil of each of the two leaves of the corm, and new root primordia differentiate in the buds. The tip of the stem dies when the corm is mature. However, when the plant is old enough to bloom, the tip continues to grow and produces an inflorescence which pushes up through the sheath of the inner leaf, and extends beyond its blade. This inflorescence consists of a peduncle and a raceme with from 6 to 12 flowers. It has not yet been determined how old a plant must be before blooming.

Development and Structure of Roots. The embryo has no primary root, hence all the roots of the plant are adventitious. The first root of the seedling arises by rapid nuclear and cell divisions in a small group of parenchymatous cells in the outer cortex of the upper part of the protocorm. The group of meristematic cells enlarges and becomes differentiated into a typical root-tip, and then elongates and extends horizontally outward. The root may stretch the epidermis before breaking it and emerging (fig. 7). The root remains unbranched. Often this root from the protocorm is absent, in which case a primordium (or occasionally two) arises in the bud. It appears as a group of meristematic cells in the outer cortex of the internode between the first and second leaves (fig. 5). This group of meristematic cells becomes a root-tip which elongates, digests its way through the epidermis of the stem and the sheath of the first leaf, and emerges. Sometimes, however, the seedling has no root (fig. 2), and absorption is then entirely accomplished by means of the epidermis and the absorbing hairs of the protocorm.

In each succeeding year, when the upper bud of the corm develops into a shoot, adventitious roots arise at its base (fig. 3). The number of roots per year increases as the plant ages. An early stage in the formation of a root primordium (figs. 9, 12, 32) shows a small group of meristematic cells in the outer part of the stem, just below the attachment of a leaf. This group of meristematic cells becomes dome-shaped, as in figure 9, and may remain dormant in this condition during the winter, or may differentiate into a typical root-tip before dormancy begins. When the bud grows in the spring, the root-tip elongates horizontally and digests its way through the epidermis of the stem and the bases of one or more leaf-sheaths which enclose it (figs. 11, 29–34). The root-tip, or tips, which originate in the lower bud of a corm do not develop into roots if this bud is inhibited in its growth by the growth of the upper bud.

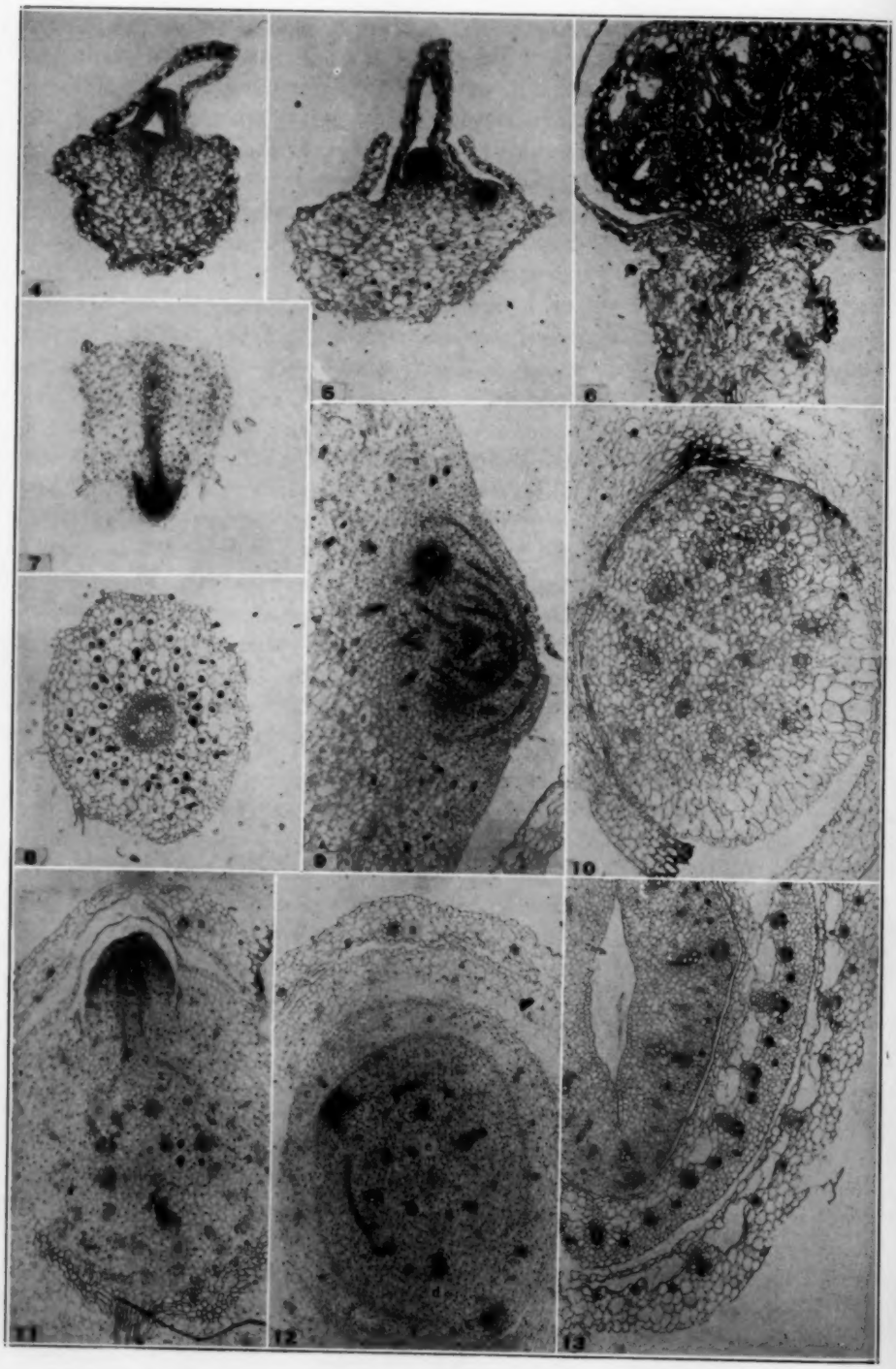
The roots of older plants form whorls in a zone at the base of the lateral shoots (fig. 3). The positions of the ten roots of a medium-sized plant are seen in figures 29–34, where the roots are numbered in the order of their position, beginning with the lowermost. This order is not necessarily the order of their age (for example, the seventh and eighth roots are younger than the ninth), but usually the lower roots are older than the upper ones. In the plant illustrated, the roots seem to be approximately opposite each other in series, that is, the first is opposite the third, the second opposite the fifth, the fourth opposite the sixth, and the seventh opposite the ninth. The eighth, however, is not opposite the tenth. Too few cases have been studied to permit generalizations concerning the regularity of the positions or the order of development of the roots. They extend outward in all directions from the shoot and are unbranched.

A mature root (fig. 8) consists of an epidermis, bearing root-hairs, a parenchymatous cortex, a well-defined endodermis, a stele with radially arranged xylem and phloem and a small pith. The endodermal cells have Casparian strips on their radial walls, and the cells of the pericycle are thin walled opposite the xylem and thick walled opposite the phloem. The exarch xylem and phloem are surrounded by sclerenchymatous cells. The number of alternating strands of xylem and phloem increases from four (tetrarch) in young roots to many (polyarch) in older ones. Hyphae of the mycorrhizal fungus, which entered through the root-hairs, form knots in many of the cells of the cortex.

Structure of Leaves. The three or four leaves of the seedling consist of two or three layers of undifferentiated mesophyll between the epidermal layers (figs. 4, 5). The outer leaf has a single median vein, and each of the others has three parallel veins, a median one and two smaller lateral ones. The cross section of the median vein shows only a few tracheids and sieve tubes, surrounded by a parenchymatous bundle sheath. The lateral veins may show only a single tracheid and one or two phloem cells in cross section.

After the first year, the shoot produces from three to five leaves each year. Only one (usually the third) bears the elongated grass-like blade by which the plant is recognized during the growing season. Its blade (limb) and sheath are separated by a joint, but no ligule is present. The lower leaves are tubular sheaths. Sometimes a smaller leaf with a diminutive blade appears above the principal leaf.

All the leaves become longer, wider, and thicker each year, and the number of veins in each increases. When young, a plant has three veins in each leaf; when older, five; then seven; and when old enough to bloom, it may have from thirty to forty veins. The larger veins enter the leaf from the stem separately, and the smaller veins arise as branches from the larger ones. All the veins are parallel, but small cross-veins connect adjacent veins at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frequent, irregular intervals. All the veins join near or at the pointed tip of the leaf.

The leaves of an individual plant differ somewhat in structure (figs. 12, 13). They are progressively thicker from the lower to the upper. In all leaves the epidermal layers are thinly cutinized, and the mesophyll consists of simple parenchymatous cells, smaller in the outer half of the leaf, and larger in the inner half, but with no differentiation into typical palisade and spongy tissue. Large air spaces appear in the inner mesophyll of the lower leaves. The veins are surrounded by sclerenchymatous bundle sheaths. The larger collateral veins contain both xylem and phloem and the smaller veins may contain only phloem. Smaller strands between the veins may be composed entirely of sclerenchyma. The main veins are progressively larger from the lower to the upper leaf.

Vascular System. The embryo has no vascular tissue, but when the apical bud is formed on the protocorm, a small central provascular strand is differentiated at the base of the bud (fig. 4) and continues upward as the bud develops. This strand becomes a simple protostele (fig. 26), its differentiation beginning at the lower end and proceeding upward. The stele is bounded by an endodermis of large thin-walled cells with conspicuous Casparian strips on their radial walls and by a parenchymatous pericycle of one layer of cells. The xylem consists of a few scalariform tracheids; the phloem

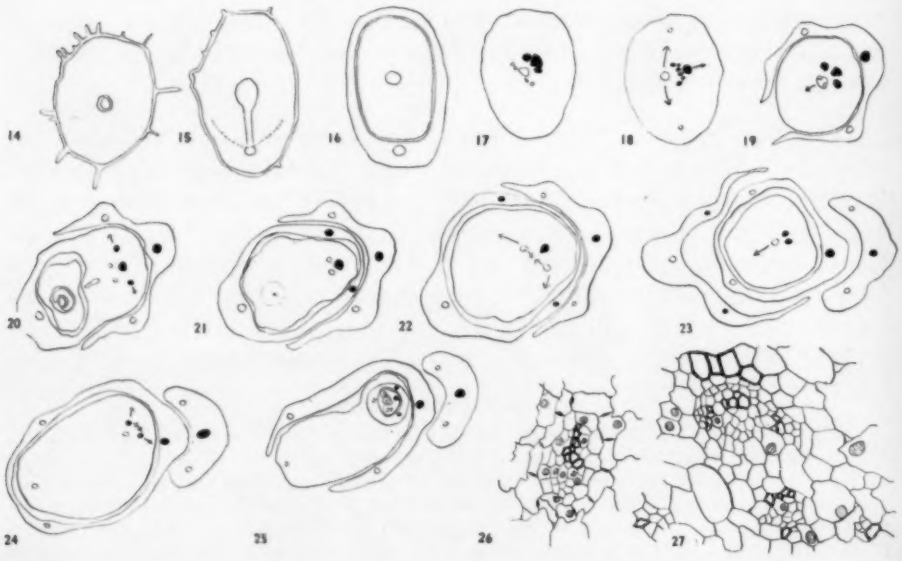
Explanation of figures 4–13.

Photomicrographs, showing structure of plant at different stages of development. Fig. 4. Median longitudinal section of a young seedling (about same age as seedling in figure 1a) showing protocorm with provascular strand, meristem of bud, primordia of two concentric leaves. Fig. 5. Longitudinal section (not median) of a seedling somewhat older than that in figure 4, showing protocorm, second leaf longer than first, primordium of third leaf, and primordium of first adventitious root below the attachment of the second leaf. Fig. 6. Longitudinal section of a seedling (about the same age as the seedlings in figure 2D, E), showing portions of protocorm (below) and second corm (above), second corm with starch, protocorm with none; thick-walled cells above and below narrow junction between 2 corms, sheaths of 2 lower leaves stretched by second corm. Fig. 7. Cross section of protocorm at level of first root, showing root protruding and stretching epidermis; provascular strand between center of root and stele of protocorm. Fig. 8. Cross section of mature root of old plant. Fig. 9. Portion of section of corm of old plant, showing bud with primordia of leaves, provascular strands, and primordium of adventitious root between first and second leaf-primordia; bud covered by corm tissue. Fig. 10. Cross section of base of shoot, just above its separation from corm. Vascular bundles from corm, each with circular strand of phloem, relatively small amount of xylem, and sclerenchymatous bundle-sheath. Fig. 11. Cross section of same shoot between first and second nodes; a, c, d, e, midrib and midrib traces of first, third, fourth and fifth leaves, respectively. Young root digesting way through epidermis of stem and outer leaf, vascular connection of root and stem. Portion of cylinder of sclerenchymatous cells, showing connection with stele of older root. Fig. 12. Cross section of same shoot at third node; letters, as above. Portions of sheaths of three leaves, young bud (upper left), provascular strands extending horizontally toward bud, root primordium (lower right) at base of third leaf, 7 large and 8 small traces to fourth leaf. Fig. 13. Portions of cross sections of three mature leaves.

consists of a few sieve tubes and companion cells. The arrangement of xylem and phloem appears to be monarch.

If a root is formed in the protocorm, a simple protostele is differentiated inward from the center of the root and meets the central stele of the protocorm at a right angle (fig. 7).

The upper part of the vascular system of the seedling consists entirely of leaf traces which make a two-sided pattern in supplying the two ranks of alternate leaves. This vascular system will be described from the base of the seedling upward (figs. 14–25) rather than in the direction of its differen-



FIGS. 14–27. Vascular system of plant of first season. FIGS. 14–25. Series of cross sections from base upward, showing course of vascular bundles. Traces originating from one main bundle in black; those from other main bundle in white. FIG. 14. Through protocorm, with protostele and absorbing hairs. FIG. 15. Trace to first leaf, at a right angle with protostele. FIG. 16. Sheathing first leaf, with one vein; one vascular strand in stem. FIGS. 17–18. First internode; larger of two main bundles (black) separated into three, median becomes median trace of second leaf, laterals each divide into two; other main bundle (white) separated into three. FIG. 19. Base of second corm above second node. Second leaf with three veins. Inner branches of two laterals (black) fused, median (white) divided into three. FIG. 20. Third node, leaf not entirely separated. Midrib of leaf and trace to bud from median of above three (white), two lateral traces (black) to third leaf. FIGS. 21–22. Above third node. Second and third leaves, three veins each; three bundles (1 black, 2 white) continuing upward. FIG. 23. Above fourth node. Larger bundle (black) divided into three, middle becomes median trace to fourth leaf; two smaller bundles (white), each divide into two, inner branches unite, outer become lateral traces to fourth leaf. FIGS. 24–25. Top of second corm. Fused bundle (white) divides into two, one goes to tip of corm and other to bud in axil of fourth leaf; two bundles (black) go to same bud. FIG. 26. Detail of protostele from figure 14. FIG. 27. Detail of bundles from figure 17.

tiation from the tip downward. The central stele of the protocorm "divides" into two unequal bundles. The smaller bundle "passes into" the first leaf (fig. 15), and the larger continues upward for a short distance and then "divides"[2] into two. The larger of these bundles, shaded black in figures 17–25, gives rise to one-half of the vascular system, and the smaller, white in figures 17–25, gives rise to the other half. Each half will be described separately.

The larger of the two main bundles divides into three (fig. 17). The median of these passes into the midrib of the second leaf, and each of the two smaller lateral ones divides again (fig. 18). The two outer of these traces become the lateral veins of the third leaf (fig. 21). The two inner bundles join into a single bundle which continues upward to the fourth node (figs. 19–22) and then divides into three. The median bundle of these three goes to the midrib region of the fourth leaf (fig. 23), and the other two go to the bud in the axil of the fourth leaf.

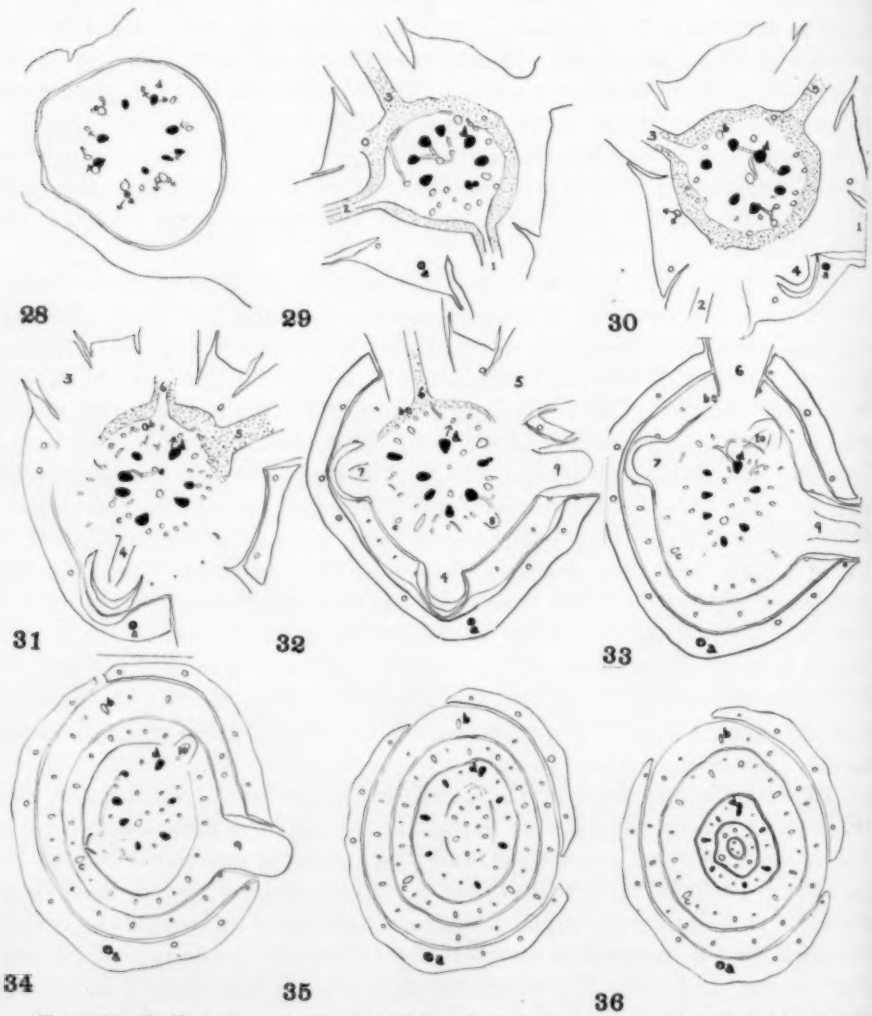
The course of the bundles on the opposite side of the seedling is similar. The smaller main bundle in the first internode divides into three (fig. 18), the two lateral ones becoming lateral traces to the second leaf, and the central one continuing upward to the second internode, where it again divides into three (fig. 20). The median one of these three divides into two, one of which passes into the midrib of the third leaf and the other of which passes into the bud at the third node (fig. 20). Each of the two lateral bundles divides into two, the outer two becoming the lateral veins of the fourth leaf; the inner two joining and continuing upward to the tip of the seedling (figs. 23–25). Thus the median traces of the second and fourth leaves and the lateral traces of the third form one-half of the vascular system, and the median traces of the first and third and the lateral traces of the second and fourth leaves form the other half of the vascular system. When the new corm is formed by the enlargement of the two upper internodes, the vascular bundles are merely separated by the enlarging cells of the parenchyma and are not changed in their course.

Because the new shoot develops from the upper bud of the corm in each subsequent season, the vascular system of this shoot is differentiated when the bud is developing on the corm, and is joined to the vascular system of the corm very early in the history of the bud. The vascular system matures as the bud grows into the new plant. Each year, as the plant becomes larger, its vascular system increases in number of bundles and complexity of pattern. The number and arrangement of vascular bundles was studied in increasingly older plants. The exact age of these plants was not known, but their

[2] The stele is said to "divide," to "give off branches" which "enter" other parts, and so forth, much as these expressions may be used of a road all built at one time, not as meaning that such events occur in ontogeny. It is in such a sense that they are used in the rest of this paper; the quotation marks being hereafter omitted.

age was assumed to be related to their size, to the number of veins in the principal leaf, and to the number of adventitious roots at the base of the shoot.

The course of the vascular bundles in an older plant—one with 10 roots and 15 veins in its principal leaf—is illustrated in the series of cross sections in figures 28–36. The upper bud of this plant had begun to develop and



FIGS. 28–36. Vascular system of older plant. Series of cross sections of developing shoot, from base upward. Letters as in figure 11. Principal bundles which enter from corm and extend to fourth leaf in black. Adventitious roots numbered in order of position from base upward. FIG. 28. Base of shoot above separation from corm, as in figure 10. Two irregular rings of vascular bundles, some branching, others fusing (indicated by

the first five roots had emerged at the base of the shoot (as in figure 3B, C) when it was fixed for sectioning. Here, again, the course of the bundles will be described from the base upward. The number of bundles in the base of the shoot varies at different levels because some bundles fuse and others divide. Twenty-one bundles are shown in figure 28. They are placed somewhat irregularly in two rings, the larger bundles in an inner ring and the smaller alternately in an outer ring. Figure 10 shows the character and arrangement of 15 similar bundles in the base of another plant. Each bundle has a circular strand of phloem, a relatively small amount of xylem, and an encircling sclerenchymatous bundle-sheath. Some appear to be either fusing or dividing.

At higher levels in the stem, the vascular system becomes very complex and seems to follow no regular pattern, as it does in the seedlings. The bundles may branch, anastomose, or connect by horizontal cross-bundles. Their course is particularly difficult to follow in the region where the roots emerge (figs. 29–32), because here they pass into and are obscured by a cylinder of cells which become thick-walled. A portion of this cylinder of sclerenchymatous cells is seen in the lower part of figure 11.

The smaller bundles in the base of the shoot supply the first ring of roots and the first leaf. These bundles branch profusely, and several neighboring branches converge and join with the provascular strands of each young root-tip (fig. 11, upper part). As the tissues in the root develop, the sclerenchyma surrounding the bundles to the root becomes continuous with that which surrounds the vascular tissues in the root (fig. 11, lower). The number of bundles which supply a root and the manner in which the collateral bundles of the stem become oriented to form the radially arranged strands of xylem and phloem in the root were not studied.

Other branches of bundles become the traces to the first leaf. These are followed with difficulty because they are obscured by the emergence of the roots below and at the level of departure of the leaf. The midrib and several

arrows). FIGS. 29–30. Below first node. First three roots emerging, cylinder of sclerenchymatous tissue (stippled), vascular bundles branching, anastomosing, and connecting by cross-bundles, traces of first leaf (ringed heavily). FIG. 31. First node. First leaf partly separated from stem, three additional roots, part of ring of traces to second leaf in cortex, two central bundles present. Photomicrograph (reversed) of portion of this section in figure 11. FIG. 32. Second node. Second leaf partly separated from stem, seventh root penetrating base of second leaf, young primordium of eighth root in cortex of stem, ring of traces to third leaf forming. FIG. 33. Second internode. Ring of traces to third leaf, ninth root penetrating first and second leaves, primordium of tenth root in cortex of stem. FIG. 34. Third node. Three sheathing leaves, axillary bud of third leaf, ring of 15 traces to fourth leaf forming, 6 bundles in center of stem continuing upward. Photomicrograph (reversed) of portion of this section in figure 12. FIG. 35. Fourth node below leaf and bud, 7 traces to fifth leaf, 2 bundles continuing upward to stem tip. FIG. 36. Tip of shoot. Five concentric leaves, with 12, 17, 21, 15, and 7 veins, respectively.

other traces, however, can be followed in figures 29 and 30. They simply pass through the cylinder of thick-walled cells, extend obliquely upward across the cortex, and enter the base of the leaf. Of the 12 strands in the first leaf, several are small, consist only of sclerenchymatous cells, and should probably not be called veins. These seem to have no connection with the bundles in the stem.

The seven larger bundles in the base of the shoot (black in figs. 28–36) also give off numerous small branches which become arranged in concentric rings and supply the other leaves and roots. One ring of 17 traces supplies the second leaf and another of 21 supplies the third (figs. 29–34). Some of these are seen in detail on either side of the root in figure 11. The seven main bundles, together with eight smaller alternating branch-bundles, finally enter the base of the fourth leaf (figs. 33–35, 12) which is the principal leaf of the plant. Two central bundles which originate below the first node become the midribs of the fifth and sixth leaves. One of these, together with six additional branch-bundles, supplies the fifth leaf, and the other goes to the tip of the stem.

The courses of the seven main bundles were followed from the corm upward to the base of the fourth leaf in order to discover a possible plan in their branching. No such plan was found. The course of the median trace to the fourth leaf (d in figs. 28–36, 11, 12) will be described. In the base of the stem it gives off two branches, one extending outward from each side (fig. 28). At a higher level, it gives off another branch (fig. 29) which enters the fifth root. Still higher it connects by a cross-bundle with one of the bundles in the center of the stem (fig. 30), and above this it connects by two cross-bundles with the two adjacent main bundles (fig. 30, dotted lines). Continuing upward, it then gives off, toward the outside, two small bundles (figs. 31, 32, arrows) which become leaf traces to the second leaf, and finally another which divides into two (fig. 33), which become traces to the third leaf. It then passes into the midrib region of the fourth leaf without further branching.

A similar study of the vascular systems of many older plants indicated that the larger bundles entering the stem from the corm extend upward, giving off many branches, and become the principal veins of the principal leaf; that usually an odd number of veins enters this leaf; that the number of veins in the sheathing basal leaves is greater than the number in the principal leaf; that the number of veins in the blade of the principal leaf is greater than the number in its sheath because some of the veins in the blade branch; that the branches from these bundles supply the other leaves and roots. The number of strands per leaf may be large; for example, the outer leaf in figure 13 has 51, the second has 58, and the third has 31. The number of principal veins in these leaves is 19, 11, and 9, respectively.

DISCUSSION

The interpretation of the structure of the embryo of orchids presents difficulties. The embryo may be considered simple and undifferentiated (Arber, 1, p. 166), lacking all of the parts of a typical monocotyledonous embryo and consisting of only a food-storage region and a meristematic region. When the seed germinates, the posterior portion of the embryo supplies food to the anterior meristematic region which produces a more or less enlarged and elongated axis with a bud at its apex. The bud develops into a stem with sheathing leaves at its nodes, and might, therefore, be considered a plumule (epicotyl?). But how shall the axis-like part, which lies between the original food-storage region and the insertion of the first leaf, be interpreted? It becomes green because of the formation of chloroplasts in the outer layers of its cortical cells. It may produce absorbing hairs all over its surface. Its central vascular strand is a monarch protostele, surrounded by a well-differentiated endodermis. The first root of the seedling often originates in this part of the seedling. Goebel (11, pp. 1402–3) calls this part of the axis a hypocotyl. It has many of the features of a hypocotyl, but if it is one, must the leaf at the first node be considered a cotyledon, or does the hypocotyl join the epicotyl with no cotyledon at the junction? I have called this part of the axis a protocorm, or first corm, simply because it enlarges in diameter and becomes filled with starch. I have assumed that the hypocotyl is lacking and that the plumule produces the shoot which bears true leaves at its nodes.

There seems to be no question about the fact that a primary root is lacking in the embryo. This absence of a root is not surprising, because the primary roots of many other monocotyledons are lacking or ephemeral. Arber (1) states that the differentiation of a primary root at the suspensor pole of the embryo is prevented by the presence of the endophytic fungus in the cells of this pole. This cannot be true of *Calopogon pulchellus* because no endophytic fungus was present in the embryos nor in seedlings grown in a sterile culture medium. All of the roots of *C. pulchellus* are adventitious, arising in the cortical parenchymatous cells of the protocorm or of the lower nodes of the stem.

Is a cotyledon present in the embryo? Some might interpret the food-storage region of the embryo as a cotyledon; others might assume that the first leaf is a cotyledon; while still others might conclude that a cotyledon is lacking. In this work I have taken the last position.

Growth of *C. pulchellus* is sympodial; that is, the new shoots arise from lateral buds. Sympodial growth is common among the orchids and other monocotyledons. The terminal bud ceases growth and differentiation and usually dies, but the causes of the cessation of growth or death of the termi-

nal bud are not known. Arber (1, pp. 29, 221), reporting work by Bernard, suggests that growth and differentiation slow down or cease when tuberization begins and that tuberization begins when the plant becomes infected with the mycorrhizal fungus. Knudson (14, 15) showed that certain effects of the fungus could be replaced by the addition of certain carbohydrates. Whether or not the cessation of terminal growth and the tuberization of the two upper internodes (with the intervening node) of the stem of *C. pulchellus* are related to infection by a mycorrhizal fungus or to the carbohydrate supply is not known.

The vascular system of the young plant consists of the single vascular bundle in the protocorm and the leaf traces, while that of older plants consists entirely of leaf traces. The single leaf trace of the first leaf "passes" independently across the cortex and joins the bundle in the protocorm at a right angle. The three leaf traces from each of the other leaves fuse in a definite pattern and form two main bundles which join with the bundle in the protocorm. The fact that the trace of the first leaf is entirely separate from those of the later leaves may be a consideration in determining whether or not this leaf is a cotyledon.

Each year after the first, the vascular system of the plant arises in the upper lateral bud of the corm. Provascular strands appear, in the usual manner, during the differentiation of the bud, and those strands to the third leaf-primordium connect with nearby bundles of the corm and become the main vascular bundles of the stem of the new plant. Those provascular strands which become the leaf traces of the first and second leaves, as well as those to the adventitious roots, join the main vascular strands very near the level of the departure of the respective organs. Leaf traces from the fourth leaf (when present) also join to the main vascular strands.

Because each year the older plant consists of only four nodes with the intervening internodes, the pattern of the vascular system is the same, except that the number of bundles increases as the plant gets older. The pattern is different from the palm type (2) and the types in the Cyperaceae and other monocotyledons described by Plowman (16). The main bundles of the plant of *C. pulchellus* "pass" continuously from the corm through two internodes and become the main traces of the third leaf, which is the principal leaf of the mature plant. All other bundles are traces which join the main bundles at the nodes. Anastomoses of bundles are frequent and follow no particular plan.

The plant passes the winter as a corm with two lateral buds. I have used the term "corm" rather than "tuber" because the enlarged stem is short, thick, and axial, and is covered by the dead bases of the ensheathing leaves.

It is similar to a corm of *Crocus*. Each year a new corm is produced by the two upper internodes of the stem and the old corm shrivels and disintegrates.

SUMMARY

1. Seeds of *Calopogon pulchellus* were germinated on a culture medium and the young plants were grown for two years. Older plants were collected in the field. The anatomy of plants from embryo to the age of blooming was studied.

2. The embryo consists of a food-storing region and a meristematic region which develops into a bud. The bud produces a seedling, with a protocorm at its base and four leaves above. The first root is adventitious and may arise from the protocorm or from the first node of the stem. A second corm arises from the two upper internodes of the stem, and the excess food passes from the protocorm to the new corm. All of the plant except the second corm dies at the end of the first growing season.

3. The plant of the second year arises from a bud at the upper node of the corm. It also produces an adventitious root at its base, four or five leaves, and a new corm from the two upper internodes of its stem. The development of the plant is much the same in succeeding years, except that the number of roots becomes greater and the leaves and the new corm become larger each year.

4. The structure of the root, stem and leaves of a mature plant, and the course of the vascular system in seedlings and older plants are described.

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A FURTHER NOTE ON THE PRODUCTION OF THIAMINE BY ACTINOMYCES

J. ARTHUR HERRICK AND CONST. J. ALEXOPOULOS[1]

In a previous paper in which the writers reported the results of studies on antibiosis between some species of *Actinomyces* and certain fungi (1), it was suggested that certain results "may very well be an indication of the presence of growth stimulating substances secreted in the agar" by the actinomycetes employed in those experiments. In a subsequent paper (2) the writers reported the production of thiamine or its precursors by *Actinomyces viridochromogenus*. In the meantime Mackinnon reported the production of thiamine by *A. albus* (3).

In view of the above, it appeared desirable to test a number of different species of *Actinomyces* to discover if the production of thiamine is widespread in this genus.

EXPERIMENTAL STUDIES

A suitable number of 200-cc. Erlenmeyer flasks, each containing 25 cc. of a liquid medium, prepared according to the formula and procedure previously reported (2), were sterilized by autoclaving at 17 lbs. pressure for 15 minutes. Ten flasks were then inoculated with a heavy spore suspension of each of 24 actinomycetes,[2] respectively. A suitable number of flasks were retained for use as controls.

Nine days after inoculation[3] the actinomycete mycelium was removed by filtration through filter paper, the filtrates restored to their original volumes with distilled water, and their acidities adjusted to pH 5.4. The 250 cc. of each filtrate were divided into 50-cc. portions and returned to five of the original flasks. The sterile control medium was treated in a similar fashion. The filtrates were now sterilized at 17 lbs. pressure for 20 minutes. In order to destroy a thermolabile inhibitor known to be present in filtrates of *A. gougeroti* cultures, these filtrates were immediately reautoclaved at 17 lbs. pressure for another 20 minutes. On the following day all flasks were inoculated with 4-mm. discs cut from young cultures of *Phycomyces blakesleeanus* growing on cornmeal agar in Petri dishes.

[1] The writers wish to express their appreciation to Dr. H. A. Cunningham, Chairman, Department of Biology, Kent State University, for his encouragement and cooperation in providing research facilities.

[2] The writers are grateful to Dr. Selman A. Waksman for supplying 14 of the 24 cultures employed in these experiments.

[3] *A. gougeroti* was permitted to grow 17 days because of its very slow growth rate. *Proa. polychromogenes* and *Micromonospora* failed to grow satisfactorily in the medium used and were discarded after several weeks.

Thirteen days after inoculation the *Phycomyces* mycelia were removed from the filtrates by filtration through filter papers, dried at 100° C, and the dry weights determined. Because of a few contaminations only four of each set of flasks were filtered. The essential data are presented in the accompanying table (table 1).

TABLE 1. *Dry weights of Phycomyces blakesleeanus mycelium produced in 13 days on culture filtrates of various actinomycetes*

Species	Dry weight, in mg., of mycelium from four flasks	Description of the *Phycomyces* mycelium
A. albidoflavus	287	Complete coverage of surface. Heavy sporangiophore production.
A. albosporeus	154	Complete coverage of surface. Medium sporangiophore production.
A. albus	206	Most of surface covered. Medium sporangiophore production.
A. annulatus	166	One-half of surface covered. Medium sporangiophore production.
A. aureus	184	One-half of surface covered. Medium sporangiophore production.
A. bobili	468	Complete coverage of surface. Very heavy sporangiophore production.
A. californicus	111	Complete coverage of surface. No sporangiophores.
A. cellulosae	170	One-half of surface covered. Medium sporangiophore production.
A. fimicarius	131	One-third of surface covered. Medium sporangiophore production.
A. flavovirens	367	Surface completely covered. Heavy sporangiophore production.
A. flavus	118	Little surface growth. Very few sporangiophores.
A. fradii	511	Complete coverage of surface. Very heavy sporangiophore production.
A. gougeroti	442	Complete coverage of surface. Heavy sporangiophore production.
A. halstedii	133	One-half of surface covered. Medium sporangiophore production.
A. madurae	106	One-half of surface covered. Light sporangiophore production.
A. purpeochromogenus	111	One-half of surface covered. Light sporangiophore production.
A. reticuli	256	One-half of surface covered. Heavy sporangiophore production.
A. scabies	340	Complete coverage of surface. Heavy sporangiophore production.
A. violaceous-ruber	228	Three-fourths of surface covered. Medium sporangiophore production.
A. viridochromogenus	191	One-half of surface covered. Medium sporangiophore production.
Proa. asteroides	132	One-half of surface covered. Medium sporangiophore production.
Proa. salmonicolor	92	One-half of surface covered. Very few sporangiophores.
Control	17	Small, completely submerged mycelia. No sporangiophores.

DISCUSSION AND CONCLUSIONS

The growth of *Phycomyces blakesleeanus* as a test for thiamine has been previously discussed (2). A comparison of the growth of *P. blakesleeanus* on the filtrates of the 22 actinomycetes employed in these experiments with that on the control medium is offered as convincing evidence that all of the actinomycetes investigated are able to produce detectable amounts of thiamine, or its precursors, in culture.

Although the species investigated constitute only about one-fifth or less of the total number of actinomycetes known, the fact that all of them gave positive results would seem to indicate that the production of thiamine is very widespread in the genus *Actinomyces*.

SUMMARY

Twenty-two actinomycetes were grown on a thiamine-free liquid medium. The cultures were filtered, the filtrates acidified and autoclaved. All of the 22 filtrates were found to support a considerable growth of *Phycomyces blakesleeanus*. It is therefore concluded that all of the 22 actinomycetes investigated produce thiamine or its intermediates or precursors in culture.

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VITAMIN DEFICIENCIES OF FIFTY YEASTS AND MOLDS

PAUL R. BURKHOLDER AND DOROTHY MOYER

This paper is a report of studies made on the growth factor requirements of thirty-three strains of yeasts representing twenty-four species, and seventeen strains of molds belonging in thirteen species. Since the vitamin requirements of microorganisms have been extensively reviewed in the recent literature, discussion of various aspects of the subject will not be given here. Our knowledge concerning vitamin deficiencies of the filamentous fungi has been well summarized by Robbins and Kavanagh (1). References to important literature dealing with the vitamin relations of yeasts may be found in a paper by the senior author (2).

Cultures of *Fomes annosus* and *Lenzites betulina* were made available through the kindness of Dr. Ross W. Davidson, Division of Forest Pathology, Bureau of Plant Industry, Washington, D. C. Dr. Alma D. Waterman, Division of Forest Pathology, Bureau of Plant Industry, New Haven, Conn., supplied cultures of *Cytospora* sp. and *Coryne sarcoides*. The species of *Trichophyton*, *Hormodendron*, *Phialophora*, and *Sporotrichon* were obtained from Dr. C. W. Emmons, National Institute of Health, Bethesda, Md. The yeast cultures were supplied by Drs. L. J. Wickerham and Kenneth B. Raper, from the Culture Collection of the Northern Regional Research Laboratory, Bureau of Agricultural Chemistry and Engineering, Agricultural Research Administration, U. S. Department of Agriculture, Peoria, Ill. Stock cultures of these microorganisms were carried on yeast-peptone-dextrose agar.

The methods employed in this study were essentially the same as those which have been reported earlier (2). The basal medium employed for cultivation of the molds and yeasts contained the following compounds in each liter of solution: dextrose C.P., 20 gm.; recrystallized asparagine, 2.0 gm.; KH_2PO_4, 1.5 gm.; $MgSO_4 \cdot 7H_2O$, 0.5 gm.; $CaCl_2 \cdot 2H_2O$, 0.33 gm.; $(NH_4)_2SO_4$, 2.0 gm.; and KI, 0.1 mg. Trace elements were added to this medium in p.p.m. as follows: B, 0.01; Mn, 0.01; Zn, 0.07; Cu, 0.01; Mo, 0.01; and Fe, 0.05. Vitamin supplements were added singly or in combination in micrograms per liter of medium as follows: thiamine hydrochloride, 200; pyridoxine hydrochloride, 200; nicotinic acid, 200; biotin methyl ester, 2.0; calcium pantothenate, 200; and inositol, 10,000. Riboflavin was generally omitted from consideration inasmuch as earlier work indicated that yeasts and molds are not commonly deficient for this vitamin.[1] The dosages of

[1] In the series of cultures set up for several human pathogens (figure 1), riboflavin (200 micrograms per liter) was included in the medium.

TABLE 1. *Growth of yeasts in a chemically defined medium with varied supplements of vitamins and liver concentrate. The values represent turbidity units of cultures grown for 72 hours at 25° C.*

Organisms	− Six vitamins	− Biotin	− Pyridoxine	− Pantothenic acid	− Nicotinic acid	− Inositol	− Thiamine	+ Six vitamins	+ Six vitamins + liver
Candida albicans 416	14	10	148	179	155	139	74	156	210
C. albicans 430	8	8	174	194	190	165	130	205	187
C. albicans 461	6	10	187	192	184	147	156	176	201
C. albicans 462	4	5	224	241	234	202	124	235	281
C. albicans 467	7	0	204	200	192	193	119	190	243
C. albicans 475	0	0	0	0	0	0	0	0	181
C. chalmersi 982	0	4	312	322	322	329	289	262	244
C. chevalieri 309	265	336	391	349	329	340	379	316	623
C. deformans 321	35	290	327	304	314	290	26	340	247
C. flareri 245	0	4	121	113	113	99	98	106	95
C. mycotoruloidea 527	0	1	144	156	148	141	61	149	170
C. parakrusei 316	0	0	162	167	157	149	157	144	182
C. stellatoidea 523	27	29	185	201	189	179	86	195	206
C. stellatoidea 524	0	0	59	63	62	61	54	59	81
C. stellatoidea 525	10	28	191	205	194	190	77	195	220
C. stellatoidea 526	25	36	194	195	193	195	92	195	245
C. zeylanoides 347	0	0	160	148	72	152	147	134	65
Chalara mycoderma 709	3	382	322	375	360	355	8	357	415
Hansenula suaveolens 838	184	174	217	203	227	180	223	172	422
Monilia albicans 414	14	16	138	168	166	151	93	156	169
M. metalondinensis 82	12	23	161	191	203	166	206	189	205
M. metalondinensis 539	12	18	188	170	174	180	121	160	211
Mycoderma lafarii 936	0	36	247	307	222	249	89	211	265
M. vini 939	0	0	0	0	0	0	0	0	124
Pichia alcoholophila 373 (after 9 days)	0	0	820	795	770	820	795	720	790

TABLE 1.—(*Continued*)

Organisms	− Six vitamins	− Biotin	− Pyridoxine	− Pantothenic acid	− Nicotinic acid	− Inositol	− Thiamine	+ Six vitamins	+ Six vitamins + liver
P. belgica 952	0	3	0	113	110	59	14	109	132
P. Dombrowskii 119	19	233	256	237	204	223	9	244	290
Saccharomyces bayanus 966	26	96	316	161	372	44	257	290	397
S. validus 972	0	0	104	76	89	62	0	117	67
Schizosaccharomyces pombe 9	4	1	107	6	1	4	114	72	193
Torulopsis dattila 171	15	157	174	178	182	184	0	153	88
T. molischiana 218	4	1	174	133	131	156	129	146	199
T. sphaerica 169	0	0	229	90	0	234	193	214	215

biotin and inositol were increased 10 fold over those employed in earlier work (2).

Nine kinds of medium were prepared for testing the growth-factor requirements of each fungus as follows: no addition of vitamins, addition of six vitamins, addition of six vitamins plus Wilson's liver concentrate (or peptone for some molds) 0.5 gm. per liter, and single omissions of each of the six vitamins (table 1). The yeasts were cultivated in liquid media. For the molds, gel-substrates were obtained by addition of 1.5 per cent purified agar to the liquid media. The agar was purified by prolonged extraction of 1 pound of agar shreds in 12 liters of 5 per cent aqueous pyridine. The leached agar was then washed twice with several liters of ethyl alcohol, and finally boiled in 10 liters of alcohol for 12 hours. After filtering in a Büchner funnel, the material was dried in large crystallizing dishes at 60° C. Essentially this same method has been employed by Robbins and Ma (3) for cleaning agar to be used in vitamin studies.

In a few experiments, silica gel was employed as a semi-solid substrate. This part of the work was performed in our laboratory by Mr. E. H. Tryon, who found certain deficiencies in *Cytospora* sp., *Fomes annosus,* and *Coryne sarcoides* with this method. The technique has been discussed recently in connection with cultivation of algae (4) and would seem to offer distinct advantages for cultivation of fungi in defined media.

All the media were adjusted to about pH 5.0 and sterilization was effected in an autoclave operated at fifteen pounds pressure for fifteen minutes. Yeast

inoculum was prepared by transferring a small amount of stock culture into 5 ml. of sterile basal medium free of all vitamins. After thorough mixing to obtain a uniform suspension of organisms, a loopful 4 mm. in diameter was used to inoculate each culture tube containing 5 ml. of one of the designated kinds of media. Duplicate sets of media were employed for each kind of fungus. Growth of yeasts was allowed to proceed for 72 hours at approximately 25° C. Growth was estimated turbidimetrically with a Klett photoelectric colorimeter.

The media for cultivation of molds were inoculated with very small amounts of mycelium or with spores transferred on a platinum wire from stock cultures grown on nutrient agar. The growth period varied from three to six weeks, depending upon the rate of development of the mold. Subcultures were made in sets of deficient media to check further upon vitamin requirements and to reduce the amounts of vitamins which may have been carried over with the inoculum. Growth of the molds was observed by direct examination.

A summary of the growth responses of thirty-three strains of yeasts is presented in table 1. The code number under each species name in the table refers to the number in the culture collection from which the yeasts were derived.

Five strains of *Candida albicans* appeared to be completely deficient for biotin, and partially deficient for thiamine. These strains were isolated originally from poultry or from human hosts. The strain 475 of *C. albicans* isolated from man appears to possess deficiency for some unidentified factor. Fair growth occurred only in the medium containing liver concentrate. The other species of *Candida*, with the apparent exception of *C. chevalieri*, were also deficient for biotin. Several of these showed partial deficiencies for thiamine, and *C. zeylanoides* gave indication of partial niacin deficiency.

In the majority of yeasts biotin is a required growth factor. Next to biotin, vitamin B_1 deficiency appears most frequently. *Pichia belgica* was found to require biotin, pyridoxine, and thiamine; its growth was improved somewhat by addition of inositol. *Saccharomyces bayanus* required some accessory biotin and inositol for maximum growth. *Schizosaccharomyces pombe* grew poorly with single omissions of biotin, pantothenic acid, nicotinic acid, and inositol. *Torulopsis sphaerica* failed to grow in the absence of biotin or niacin and also showed partial deficiency for pantothenic acid.

Candida deformans, *Chalara mycoderma*, and *Pichia Dombrowskii* appear to be deficient for thiamine but not for biotin. *Candida chevalieri* and *Hansenula suaveolens* showed no deficiency for any of the six vitamins, though much better growth of these species was obtained with liver supplement added to medium containing the six vitamins. *Mycoderma vini* grew in medium containing liver concentrate but not in the synthetic media.

The essential growth factor requirements of seventeen fungi are shown in table 2. It appears from the results of our work and that of others that

TABLE 2. *Vitamin requirements of molds grown in synthetic medium containing purified agar or silica gel and varied supplements of six vitamins, etc.*

Species	Vitamin requirements	Growth in liver or peptone
Hormodendron pedrosoi	Deficient for thiamine	Somewhat stimulated
Phialophora verrucosa	Deficient for thiamine	.....
Sporotrichon schencki	Deficient for thiamine	Not stimulated
Trichophyton acuminatum	Partially deficient for thiamine	Not stimulated
T. faviforme	Deficient for thiamine and inositol	Stimulated
T. mentagrophytes 514	No deficiency observed	Stimulated
T. mentagrophytes 517	No deficiency observed	Not stimulated
T. mentagrophytes 598	No deficiency observed	Not stimulated
T. mentagrophytes 599	No deficiency observed	Not stimulated
T. mentagrophytes 607	No deficiency observed	Not stimulated
T. rubrum	No deficiency observed	Somewhat stimulated
T. sulphureum	Deficient for thiamine	Not stimulated
T. violaceum	Deficient for thiamine	Greatly stimulated
*Fomes annosus**	Deficient for thiamine	.....
*Coryne sarcoides**	Deficient for thiamine and biotin	.....
*Cytospora sp.**	Deficient for thiamine	.....
Lenzites betulina	Deficient for thiamine	.....

* Cultivated by E. H. Tryon in nutrient silica gel.

the various species of *Trichophyton* differ in their vitamin requirements. The five strains of *T. mentagrophytes* and *T. rubrum* seem to be able to grow well without the addition of any vitamins. Four other species of *Trichophyton* require thiamine, and *T. faviforme* appeared to be deficient for both thiamine and inositol. Robbins, Mackinnon and Ma (5) have recently found *T. discoides* to be deficient for thiamine, inositol, and pyridoxine. As indicated in table 2, the species of fungi which live in wood, *Cytospora* sp., *Fomes annosus*, and *Lenzites betulina* are deficient for thiamine, while *Coryne sarcoides* requires both thiamine and biotin.

SUMMARY

Vitamin requirements of thirty-three yeasts and seventeen molds, including some important pathogens in both groups, were studied in chemically defined media. Biotin and thiamine deficiencies occurred most commonly.

Deficiencies for pyridoxine, pantothenic acid, inositol, and nicotinic acid were found in several yeasts.

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INFLUENCE OF TEMPERATURE ON THE INFECTION OF WHEAT BY THE POWDERY MILDEW ERYSIPHE GRAMINIS TRITICI[1]

ROBERTSON PRATT

Discovery and recognition of physiologically specialized forms in the powdery mildews (Neger 1902, Marchal 1902) similar to those then recognized in the rusts and smuts initiated an avid search for more examples of such specialization in this group of obligate ectoparasites. Consequently, papers describing new species or races or extending our knowledge of the host range of these fungi are numerous, while there is a relative dearth of literature concerning other phases of their physiology. The purpose of this investigation was to study quantitatively the effects of temperature, daily period of illumination, and of humidity upon the infection of wheat, *Triticum vulgare*, by the powdery mildew, *Erysiphe graminis tritici*. The present paper is concerned with the effects of temperature.

METHODS

Hanging drop cultures were employed for studies involving the fungus alone. For experiments involving mildew cultures on the host plant under controlled conditions, a thermostatic chamber (Trelease 1925) was employed. Uniform light was provided by a 1000-watt clear Mazda-C electric light lamp and a reflector. To exclude extraneous daylight the light assembly was surrounded by a truncated pyramid of galvanized iron that rested on the top of the incubation chamber. Between the lamp and the glass roof of the chamber was a water screen 25 mm. deep flowing at a rate of approximately 3.2 liters per hour. To insure uniform quality and quantity of radiation, bulbs were discarded after 500 hours of service. Tests showed that mildew response and development were, as far as could be determined, identical throughout this period.

Stock cultures of the mildew were maintained in the greenhouse at 16°–21° C, and experimental plants were inoculated in the manner described by Trelease and Trelease (1928). Experimental plants were grown in mildew-free chambers or under bell jars, and all reasonable precautions were taken to avoid accidental inoculation. At the beginning of each experiment one-half of the plants were inoculated. The remainder were left in a mildew-free chamber in which conditions favorable for mildew development were maintained. If no infection appeared among the control plants within

[1] The work reported in this paper was done in the laboratory of Plant Physiology at Columbia University between 1931 and 1935.

five days, it was considered as reasonably certain that the whole set of plants was mildew-free at the start of the experiment. At the temperature used (16°–21° C), mildew becomes abundant on an infected plant in from two-and-one-half to three-and-one-half days. These plants were then inoculated and used for stock cultures of the fungus. All experimental plants were inoculated at about the same time of day (5:00–6:00 p.m.), so that the photosynthetic and metabolic products within the plants would be as nearly uniform as possible at the time of inoculation in the different experimental sets. Yarwood (1934) has shown that clover leaves removed in the evening are more susceptible to *Erysiphe* than those removed in the morning. Detailed methods and deviations from this general mode of procedure are noted under the experiments concerned.

A virulent strain of mildew which had been maintained in the greenhouse for several years was used. It was not deemed necessary to make a single-spore isolation of the mildews, since very consistent and reproducible results were obtained in all experiments, indicating that if two or more strains of the fungus were present they were equally and similarly sensitive to the experimental conditions imposed upon them. In all experiments, Marquis, a Spring variety of wheat was used as the host. Plants were grown in ordinary loam in four-inch clay pots, about 50 plants in a pot, and were inoculated when the first leaf was fully expanded.

RESULTS

Table 1 and figure 1 show the effect of temperature upon mildew development on wheat plants exposed to twelve hours illumination daily. In all temperature experiments eight pots of plants (about 400 seedlings) were used and each experiment was duplicated. Thus the averages are for 16 sets of plants. High humidity was provided by hanging water-soaked towels around the inside of the incubation chamber. The data in table 1 indicate that the optimum temperature for mildew infection on wheat under the conditions of these experiments is about 20° C. From −2° to 15° C the rate of mildew growth increased rapidly and the effect of temperature on the relative rates of early and late stages of development was about the same (column 5), although the maximum virulence of infection at −2° C was somewhat less than at higher temperatures (column 6). At the optimum temperature (20° C) the processes concerned with maturation and the formation of conidia proceeded relatively about twice as rapidly as at the lower temperatures (column 5). A slight further rise in temperature, however, while not appreciably altering the rate of early growth (column 2) exerted a relatively pronounced effect on the stages of development concerned with vegetative maturation (column 5). At 30° C no macroscopic indications of infection were found.

TABLE 1. *Effect of temperature upon incubation period (time required for mildew to appear) and maturation period (time required for development of conidia minus incubation period)*

(1) Temp.	(2) Average incubation period[a]	(3) Average time for appearance of conidia	(4) Average maturation period[b]	(5) Maturation Period / Incubation "	(6) Virulence of infection (approximate)
−2°C	17.5 days	28.25 days	10.75 days	0.614	+++
+5°C	9.75 "	16.00 "	6.25 "	0.642	++++
10°C	6.25 "	10.00 "	3.75 "	0.600	++++
15°C	3.25 "	5.25 "	2.00 "	0.615	++++
20°C	2.50 "	3.25 "	0.75 "	0.300	++++
25°C	2.50 "	3.75 "	1.25 "	0.500	++++
30°C	.....	.....	.....	.....	.....

[a] Time elapsed between inoculation of the plants and the first macroscopic signs of infection.

[b] Time required for appearance of first conidia minus incubation period.

Compared with many saprophytic and parasitic fungi, *Erysiphe* appears to have a very low maximum temperature for infection, although Maneval (1922) reported that for twenty species of rusts the maximum temperature for germination of teliospores is less than 30° C. High temperature might prevent infection by a direct deleterious effect upon the fungus either before, during, or after germination of the conidia or by causing changes in the metabolic products or processes of the host that render it unsuitable for supporting the parasite. These possibilities were examined.

Large numbers of conidia were used to determine the effect of temperature upon spore germination in tap water. Hanging drops containing from two to three hundred spores each were kept in darkness at the different temperatures and after twenty-four hours the spores were killed by placing a little formalin in the bottom of the chambers. The total number of spores and the number of germinated spores were then recorded. The data obtained are presented in figure 2, which shows that maximum germination occurred from 15° to 20° C. Either side of that range, germination fell off abruptly. At 35° C there was no germination at all in twenty-four hours, and the spores lacked their natural clear hyaline appearance. Instead, the contents appeared granular and coagulated. The effect of temperature upon spore germination will be referred to below. It suffices here to note that failure to obtain infection of wheat at 30° C was not due to failure of spores to germinate, since germination at that temperature was of the same order of magnitude as at −2° C, where good infection occurred.

Wheat plants grown from seed at 30° C until the first leaf was fully expanded were inoculated, and at regular intervals two pots of the inoculated plants were transferred to a chamber at 20° C and the remainder were left at 30° C. Minute white patches of mycelium appeared in two and a half days and numerous conidiophores appeared a day later on the plants at 20° C,

but no signs of mildew appeared on those at 30° C even after one week. Microscopic investigation of these leaves revealed no stages of mildew development beyond the production of germ tubes from thirty to forty microns in length. No penetration of the host tissue by the fungus could be found. It may be concluded from these experiments that exposure of wheat seedlings to a temperature of 30° C for the first five days of growth does not produce any change which seriously impairs their normal capacity for supporting mildew

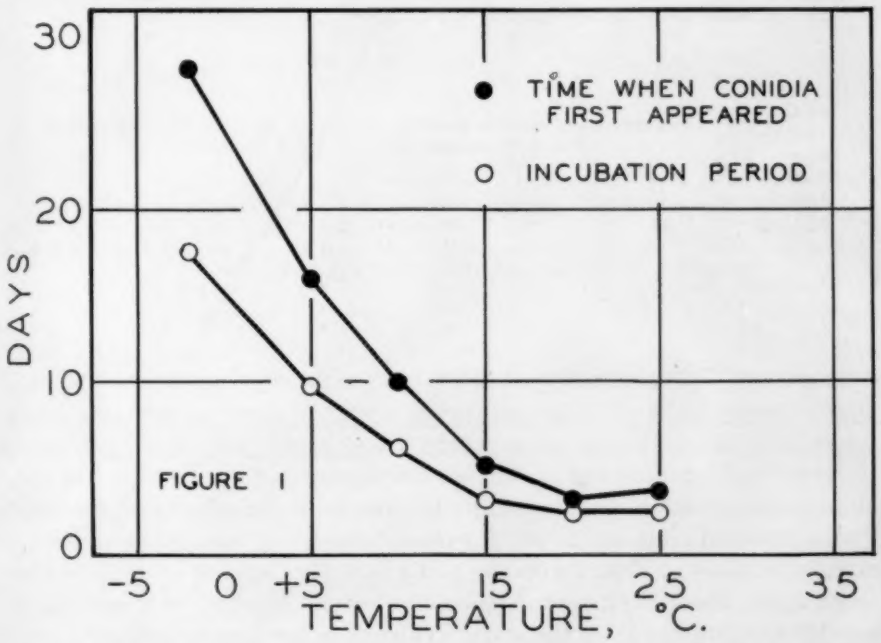

FIG. 1. Time required for development of mildew infection on wheat plants at different temperatures.

(table 2). In another experiment, plants were grown at 20° C until the first leaf was expanded. Then the plants were inoculated. Half the pots were kept at that temperature, while the remainder were removed to a thirty-degree chamber. Each morning and evening (8:30 a.m. and 6:30 p.m.) thereafter, two pots from each set were exchanged—i.e., two from the lower temperature were removed to the thirty-degree chamber and vice versa. The results are presented in table 2.

Two-and-one-half days after inoculation the plants continuously at the lower temperature from the start had minute patches of mycelium on them and one-and-one-half days later numerous conidiophores. Plants left at 20° C less than forty-eight hours before transference to 30° C showed no macroscopic signs of infection after four to five-and-one-half days at the higher

TABLE 2. *Effect of transferring plants grown at moderate and high temperatures to high and moderate temperatures, respectively, at regular intervals after inoculation*

Days at 20° C after inoculation	Development of mildew on plants grown at 20° C and transferred to 30° C at regular intervals after inoculation
0.0	No macroscopic signs of mildew on any of these plants after 5.5 days
0.5	" " " " " " " " " " " " 5.0 "
1.0	" " " " " " " " " " " " 4.5 "
1.5	" " " " " " " " " " " " 4.0 "
2.0	Small white tufts of mycelia present after 3.5 "
2.5	" " " " " " " " 3.0 "
3.0	" " " " " and a few conidia after 2.5 "

Days at 30° C after inoculation	Development of mildew on plants grown at 30° C and transferred to 20° C at regular intervals after inoculation
0.0	Few small mycelial patches present after 2.5 days, conidia after 3.5 days
0.5	" " " " " " 2.5 " , " " " " "
1.0	" " " " " " 3.0 " , few conidia after 5.0 days
1.5	No mildew development macroscopically apparent after 5.0 days
2.0	" " " " " " 5.0 "
2.5	" " " " " " 5.0 "
3.0	" " " " " " 5.0 "

temperature. Those transferred after forty-eight or sixty hours had only minute white flecks after an additional eighty-four or seventy-two hours, respectively, at the higher temperature. These plants were then returned to the lower temperature, but no further development of the mildew occurred. Microscopic examination showed the hyphae to be shrunken and shriveled. Plants removed from 30° to 20° C twelve hours after inoculation developed mycelial patches on their leaves two and a half days later or three days after inoculation. These plants never became so heavily infected as those at a favorable temperature from the start. Evidently a few spores and germ tubes were capable of withstanding the high temperature for several hours and when they were placed in favorable conditions they established infection. Similarly, plants at 30° C for twenty-four hours after inoculation showed sparse mycelia three days later, or four days after inoculation. A few conidia appeared six days after inoculation. From these results it seems safe to conclude that the harmful effect of high temperatures is primarily a direct one on the fungus and that the host plant is not directly involved.

Figure 2 indicates the effect of temperature upon the germination of conidia in tap water. A net micrometer was used for counting, and only spores within a given area in the center of each drop were counted. This precaution reduced the error which might have arisen, from differential exposure of spores in different regions of the drop, if all spores in a given drop had been counted. The controls indicated that about 1.5 per cent of the spores in a drop might already have germinated at the time of mounting the prepa-

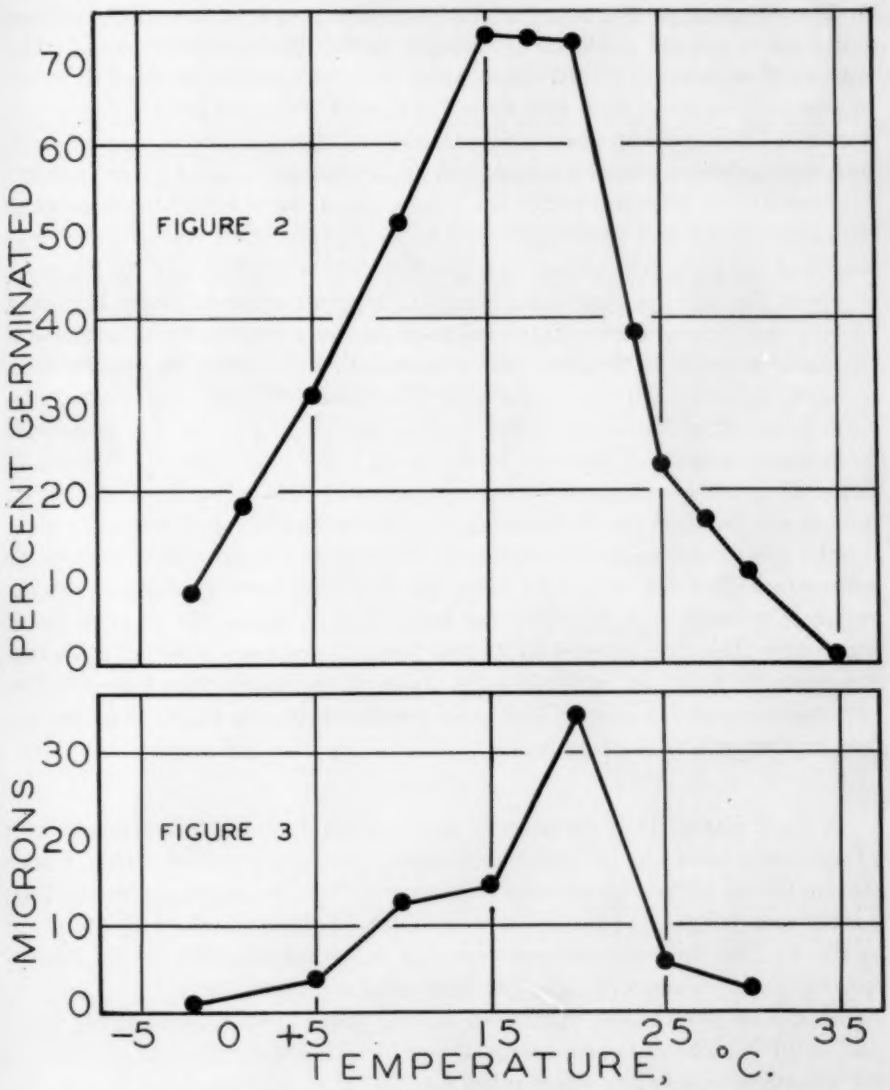

FIG. 2. Influence of temperature upon germination of powdery mildew spores after 24 hours in tap water. FIG. 3. Influence of temperature upon growth of the germ tube of powdery mildew conidia in tap water 48 hours.

ration. Therefore germination percentages below this figure,—i.e., 35° C—represent no germination at all. A comparison of figures 1 and 2 shows that infection does not occur over as wide a range as germination. This is due to failure of the parasite to penetrate into the host tissue at temperatures over 25° C.

The hanging drop method of investigating spore germination has been subjected to adverse criticism by Duggar (1901), Doran (1922), and McCallan and Wilcoxon (1932). However, since large numbers of spores distributed in many drops were used and since the figures obtained were easily reproduced in later experiments under similar conditions, it seems reasonable to consider the data that are plotted in figure 2 reliable.

Perhaps, as Brown (1922) has suggested, a more accurate measure of the early growth and development of a fungus is obtained from the average length of the germ tubes than from the percentage of germination. Figure 3, in which the average germ-tube length in microns after 48 hours is plotted against the temperature is intended to show the relation of temperature to the early growth of *Erysiphe* as indicated by this criterion. Spores were mounted in hanging drops of tap water and measurements were made forty-eight hours after mounting. After longer periods of time it was impossible to measure accurately the specimens at 15°, 20°, and 25° C. Mycelia of *Erysiphe graminis* regularly penetrate a susceptible wheat leaf in twenty-four to seventy-two hours depending on the temperature. These data show that by this criterion also the optimum temperature is 20° C and that as the temperature differed from that value the mildew growth decreased. The decrease in growth was, however, far more abrupt above 20° C than below that point. The data plotted in figures 2 and 3 are essentially alike in that development drops off more abruptly above the optimum than below it. The germination curve, however, indicates a wider optimum range than the one for early growth of the fungus.

SUMMARY

A study was made of the effect of temperature upon the infection of wheat (*Triticum vulgare*) by the powdery mildew, *Erysiphe graminis tritici*. Under the conditions of the experiments (12 hours of illumination daily from a 1000 watt Mazda lamp and high relative humidity) infection occurred from −2° to 25° C. The optimum temperature for infection was 20° C. No macroscopically visible signs of infection were observed above 25° C.

Spores of the fungus suspended in tap water germinated readily from −2° to 30° C. The optimum temperature for the germination of spores and for growth of the young germ tubes was 20° C.

Failure of wheat plants to become infected at 30° C was due to inability of the young fungus mycelium to tolerate the high temperature.

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NOTES ON PLANTS OF THE PACIFIC ISLANDS—III[1]

F. R. FOSBERG

In this paper are presented taxonomic, nomenclatural, and distributional notes on plants from the Hawaiian Islands, the New Hebrides, and Christmas Island. New species, varieties, combinations, or names are proposed in *Anectochilus, Gouldia, Timonius, Coprosma,* and *Dubautia,* with general notes on *Nephrolepis, Adiantum, Lygodium, Azolla, Cyperus, Portulaca, Spergularia, Leucaena, Phaseolus, Abutilon, Hibiscus, Malachra, Maurandya, Ruellia, Gouldia, Coprosma, Borreria, Richardia, Elephantopus, Pseudelephantopus, Ageratum,* and *Solidago.* Herbarium abbreviations are BISH for Bishop Museum, F for Field Museum, A for Arnold Arboretum, D for Otto Degener private herbarium, HARV for Harvard Botanical Museum, US for U. S. National Herbarium, and USNA for U. S. National Arboretum.

POLYPODIACEAE

NEPHROLEPIS BISERRATA (Sw.) Schott. This is the fourth species of this genus to be found in the HAWAIIAN ISLANDS. It was found growing on OAHU, probably indigenous, in a small pit in coral limestone on the Ewa Coral Plain, Jan. 12, 1936, *Fosberg 12806* (BISH) (det. R. C. Benedict).

NEPHROLEPIS BISERRATA var. FURCANS Hort. This remarkably stable horticultural variety has become established and forms a considerable colony around the abandoned settlement at the mouth of Wailau Valley, MOLOKAI, Dec. 28, 1936, *Fosberg 13453* (BISH) (det. R. C. Benedict).

NEPHROLEPIS CORDIFOLIA (L.) Presl. Although this species has been commonly regarded by previous writers as introduced in the HAWAIIAN ISLANDS, its frequent occurrence as a part of the undisturbed cloud forests of the mountain ranges, and its absence from the lowlands indicate that it is in all probability native. This fern was reported from the Hawaiian Islands by Edward Bailey in *Hawaiian Ferns,* 48 (1882). The following collections (except *Topping 3808*) were kindly determined by R. C. Benedict. LANAI: Lanaihale ridge, *Fosberg 12437* (BISH). MOLOKAI: top of cliff at head of Wailau Valley, *Fosberg 13368* (BISH). OAHU: Koolau Mts.: top of cliffs at head of Haiku Valley, Heeia, *Fosberg 13870* (BISH); peak at head of Waiawa trail, *Fosberg & Hosaka 13912* (BISH); main divide between Waikane Valley and Waikakalaua Gulch, *Fosberg & Hosaka 13928* (BISH); main divide near top of Castle Trail, Kaipapau, *Fosberg & Hosaka 13954* (BISH); crest of mountains above Kaipapau Gulch, *Fosberg & Egler 14227* (BISH); Laie Trail, Kakawainui-Ihiihi ridge, Laie, *Fosberg 14235* (BISH, USNA); Mauka Laie, Gold Brick Hill, *Topping 3808* (USNA).

[1] See Bull. Torrey Club 65: 607–614. 1938; 67: 417–425. 1940.

KEY TO HAWAIIAN SPECIES OF NEPHROLEPIS

A. Pinnules linear-lanceolate, attenuate toward apex, frond flat.
  B. Rhachis densely tawny or rusty woolly ..... *N. hirsutula* (Forst.) Presl (on the basis of Degener, Flora Hawaiiensis 17: NH, 9/9/'38 and of *Topping 2705* (USNA))
  BB. Rhachis not densely woolly, somewhat scaly or scurfy. *N. biserrata* (Sw.) Schott (form with apices of pinnules forked is var. *furcans* Hort.)
AA. Pinnules oblong or oblong-lanceolate, acute to rounded at apex.
  C. Frond flat, narrow, 5 cm. or less wide, glossy above, pinnules oblong, rhachis densely covered with red-brown scales, stolons often tuberiferous ..... *N. cordifolia* (L.) Presl
  CC. Frond trough-shaped, usually broader, rhachis thinly tawny scaly, stolons not tuberiferous ..... *N. exaltata* (L.) Schott

ADIANTUM CUNEATUM Langsd. & Fisch. Some of the Hawaiian material commonly referred to *Adiantum capillus-veneris* L., regarded as native in the islands, is to be referred to the introduced *A. cuneatum*, probably escaped from cultivation. Dr. W. R. Maxon informs me that a reliable key character for distinguishing the two is that in *A. cuneatum* the veins of the sterile pinnules end in the sinuses between the teeth while in *A. capillus-veneris* they end at the apices of the teeth. Completely fertile specimens are often difficult to determine.

HAWAIIAN ISLANDS: HAWAII: Hills above Akaka Falls, Honomu, Dec. 8, 1933, *Fosberg 10470* (BISH, USNA). OAHU: Carter Ranch, upper Manoa Valley, Honolulu, Sept. 26, 1932, *Fosberg 8861* (BISH, USNA); Niu Valley, June 4, 1932, *Topping 3532* (USNA); Honolulu, cultivated, April 1, 1933, *Fosberg 9376* (BISH, USNA).

SCHIZAEACEAE

LYGODIUM JAPONICUM Sw. This climbing fern may be reported as semi-established around an old garden at Puueo, Hilo, HAWAII, Aug. 6, 1936, *V. O. Fosberg 34* (BISH).

SALVINIACEAE

AZOLLA FILICULOIDES Lam. This floating water fern appeared in the taro patches and irrigation ditches of OAHU about 1934, and soon became extremely abundant. H. L. Lyon has told me that in 1926 he introduced *Azolla caroliniana* into the islands at the request of the mosquito abatement committee. The latter plant evidently did not become established, though the one now common in the taro patches has been misidentified as that species. Examination of fruiting specimens (*Fosberg 13833*) of the plant now in the islands shows that it is *A. filiculoides*, which has, among other characters, non-septate glochidia or barbed hairs on the microspore masses, rather than septate ones as in *A. caroliniana*.

HAWAIIAN ISLANDS: OAHU: Honolulu, Waikiki, *Fosberg 13815* (BISH); Honolulu, Manoa Valley, May 22, 1937, *Fosberg 13833* (BISH, USNA).

ORCHIDACEAE

Anectochilus apiculatus L. O. Williams and F. R. Fosberg, sp. nov. Herba pallide viridis; flos pallide flavo-viridis, calcari extus non valde

geminato, mesochilo subtus laterale bidentato, anthero apiculato, mesochilo epichiloque quam in *A. sandvicenso* valde brevior.

Pale green herb with succulent ascending or subdecumbent stems up to 25 cm. long, 3–5 mm. thick, glabrous except the inflorescence, prostrate and rooting at nodes in lower portion; leaves ovate to elliptic-ovate, 5–8 cm. long, 2.5–4 cm. wide, apex obtuse to acutish, base rounded to subcordate, narrowed to a distinct membranous petiole 3–10 mm. long, expanded and inflated below into an amplexicaul sheath about 1 cm. long on the petiolar side, 4 mm. long on the reverse, lamina membranous; spike 5–10 cm. long on a peduncle 3–5 cm. long, uppermost 1 or 2 leaves reduced to bracts; flowers somewhat loosely arranged, subtended by ovate scarious membranous bracts about 10 mm. long, about as long as the ovary and enclosing it at base; flowers pale yellowish green, about 12–15 mm. long, ovary lance-ovoid, about 10 mm. long, 1.5–2 mm. thick near base, apex subacuminate, tending to be incurved, dorsal sepal ovate, 4.5 mm. long, blunt and slightly cucullate at apex, lateral sepals 6 mm. long (over all), obliquely oblong-orbicular, obtuse, with base obliquely cordate, greatly enlarged on lower side, this basal lobe subsaccate, margins entire, texture membranous; petals 4.5 mm. long, sublunate-ovate, bluntly subacuminate, membranous, margins erose; lip 7.5 mm. long, with a short pouch-like spur 2 mm. long, enclosed by the bases of the sepals, spur scarcely geminate externally, divided within into two cavities by a longitudinal septum, each cavity containing a suberect finger-shaped callosity, mesochile 5 mm. long, about 1.5 mm. wide but inrolled into a tube, with 2 forward-pointing pairs of sub-fleshy teeth about two thirds the distance from base on lower side of the mesochile, distal pair 0.75 mm. long, lower pair 0.5 mm. long, epichile obcordate, 4 mm. wide, 2.5 mm. long, sinus 1.5 mm. deep, lobes rounded; column 2.5 mm. long; anther ovate, 3 mm. long, somewhat apiculate, twisted slightly to one side, brown with whitish margins, cymbiform; fruit fusiform, 1 cm. long, 3 mm. thick, green.

HAWAIIAN ISLANDS: MOLOKAI: head of Wailau Valley, trail up Waiakeakua-Waiokeela ridge, on steep ridge shaded in wet forest, alt. 750 m., Dec. 27, 1936, *Fosberg 13448* (HARV—TYPE, USNA, BISH).

This species may be distinguished from the commoner *A. sandvicensis* by its smaller, greenish rather than bright yellow flowers, lip with spur not conspicuously geminate externally, with mesochile conspicuously shorter and with two pairs of subfleshy teeth on the lower side rather than many or no membranous ones, with epichile much shorter, and the anther apiculate rather than acute.

A somewhat similar plant was found in wet woods in the mountains behind Hauula, Oahu, some years ago by Mr. H. Morley, but the specimen was unfortunately lost.

CARYOPHYLLACEAE

SPERGULARIA MARINA (L.) Griseb. Spic. Fl. Rummel, et Bith. **1**: 213. 1843. *Arenaria rubra* β marina L. Sp. Pl. 423. 1753. *Arenaria marina* Allioni, F. Pedem. **2**: 114. 1785. *Spergularia salina* J. & C. Presl, Fl. Cech. 95. 1819.

The correct name for the plant referred by me to *Spergularia salina* in a previous paper (Occ. Pap. Univ. Haw. **32**: 5. 1937) is *S. marina*. For further synonymy and discussion see Rossbach, Rhodora **42**: 123–137 (1940).

MALVACEAE

MALACHRA ALCEIFOLIA Jacq. Collect. **2**: 350. 1788; Ic. Rar. **3**: *pl. 549.* 1786–1793. *Malachra rotundifolia* Schrank, Pl. Rar. Hort. Mon. *pl. 56.* 1819.

A coarse, hispid herbaceous perennial 0.5–2 m. tall; stems with close stellate pubescence as well as sparse long stiff hairs; leaves 7–10 cm. across, roundish in general outline, shallowly 5-lobed, palmately veined, subcordate, obtuse or acutish, irregularly serrate, somewhat pubescent on veins, petioles 5–9 cm. long, closely stellate-pubescent; stipules filiform, about 15 mm. long, sparsely hirsute; flowers yellow, in compact axillary clusters on peduncles up to 15 mm. long, these densely stellate-pubescent, clusters surrounded by 3–4 broadly cordate bracts, these somewhat lobed, acute, sparsely hirsute, variegated; flowers few in a cluster, calyx about 6 mm. long, tube white, striped with brown, lobes lanceolate, long-hirsute; corolla hairy 12–15 mm. long; stigmas irregular in shape, ovary 5-celled, ovules 1 in a cell; fruit subglobose, splitting into 5 parts, these 3 mm. long, larger distally, puberulent, light brown with darker reddish-brown veins, splitting open along the lower two thirds of the inner angle; seeds dull sooty brown, same shape as carpel, free from carpel wall.

HAWAIIAN ISLANDS: OAHU: Kawailoa School, Waialua, Oct. 1936, *A. Miyake* (BISH, USNA).

Found growing in a vacant lot; a native of tropical America evidently recently introduced into Hawaii.

SCROPHULARIACEAE

MAURANDYA ERUBESCENS (Don) Gray. The plant usually called *Maurandya scandens* in the Hawaiian Islands, an introduced vine with densely pubescent leaves, has been identified by Dr. F. W. Pennell as *M. erubescens*, a native of Mexico. The true *M. scandens* is a glabrous plant.

HAWAIIAN ISLANDS: HAWAII: Volcano Road near Naalehu, alt. 200 m., *Fosberg 10140* (BISH, USNA). OAHU: near H. S. P. A. Arboretum, Carter Ranch, Manoa Valley, *Fosberg 8859* (BISH, USNA); *Fosberg & Duker 8940* (BISH).

ACANTHACEAE

RUELLIA GRAECIZANS Backer, Brittonia **3**: 85. 1938. This plant has been called *R. amoena* Nees and *R. ventricosa* Kunth, but neither of these names is valid. It is a small herbaceous species with dark green ovate to lanceolate leaves and horizontal tubular red flowers. It has become rather common as a garden weed in various parts of Honolulu and has been said to occur on Maui, but the Maui report is not substantiated by a specimen. I am indebted to Mr. E. C. Leonard for calling my attention to Backer's publication.

HAWAIIAN ISLANDS: OAHU: Honolulu, *Fosberg 14222a* (BISH).

RUBIACEAE

GOUDIA Gray. Since the publication of my revision of this Hawaiian genus (Bish. Mus. Bull. **147**: 1–82. 1937) the following observations have accumulated, and a number of typographical errors have been detected, which are here listed with corrections.

p. 4—footnote—for 181 read 81
p. 19—line 23—for 77 read 80
p. 20—line 9—for 58 read 62
line 11—for 62 read 58
line 46—for 58 read 61
p. 21—line 2—for 82 read 97
line 7—for 40 read 43
p. 22—line 45—for 82 read 83
line 49—for 81 read 82
p. 43—line 17—for 12782 read 12781
p. 25—in the synonymy of *Gouldia terminalis* insert *Hedyotis chamissoniana* Steud. Nom. ed. 2, **1**: 727, 1840.

GOULDIA on the island of LANAI: The recovery of the forests on the island of Lanai after almost complete destruction by introduced grazing animals (see Fosberg, Mid-Pacific Mag. April–June **1936**: 119–123. 1936) has, in all probability, resulted in a forest of considerably different floristic composition from that originally existing there. However, there is no way of demonstrating this conclusively, as we know little about the original forest.

During a visit to Lanai in 1935 I made rather extensive collections of *Gouldia*, making a particular search for the several varieties known from earlier collections. It was thought that a search especially for *Gouldia* should easily reveal all varieties which had turned up previously in more general collecting.

Complete identification of the specimens collected on this trip has shown that some varieties are very rare, while one was not found at all. *G. terminalis* var. *pseudodichotoma* was represented only by *Fosberg 12411; G. terminalis* var. *lanai* only by *Fosberg 12579; G. terminalis* var. *subcordata* by three collections, *Fosberg 12599, 12412,* and *12606. Fosberg 12502* seems to be a hybrid, *G. terminalis* var. *subcordata* × var. *pseudodichotoma,* and *Fosberg 12572* another, *G. terminalis* var. *subcordata* × var. *bobeoides. G. terminalis* var. *bobeoides* was not represented at all in the collection excepting possibly as one parent of this latter hybrid and one mentioned below. The above collections all came from the gulches, in sheltered localities.

The plants from the ridges and summits, where *Gouldia* was quite abundant, were, with the exception of one collection, all *Gouldia st.-johnii* var. *munroi* or hybrids between this and varieties of *G. terminalis.* All collections of *G. st.-johnii* var. *munroi* numbering fourteen, came from ridges and summits, where some grew in much-exposed places. It is one of the really abundant plants in the scrub forest that is revegetating these ridges. Whether in the original forest this distribution was characteristic, or whether *G. st.-johnii* is a very aggressive plant and especially able to colonize denuded areas is difficult to know. Unfortunately we have a very incomplete picture of the original forest covering of Lanai. It should be remembered that *G. st.-johnii* var. *typica,* of Oahu, is a plant of exposed ridges and summits.

Of hybrids involving *G. st.-johnii* var. *munroi* two were represented by one collection each and were found in gulches only. These were *G. st.-johnii* var. *munroi* × *terminalis* var. *bobeoides* (?), *Fosberg 12495,* and *G. st.-johnii* var. *munroi* × *terminalis* var. *lanai, Fosberg 12584. G. st.-johnii* var. *munroi* × *terminalis* var. *pseudodichotoma* is represented by four collections, nos. *12398, 12373, 12484,* and *12594.* The first three were on ridges, the last in a

gulch bottom. *G. st.-johnii* var. *munroi* × *terminalis* var. *subcordata* is represented by ***Fosberg 12477*** and *12482*, both from ridges.

A set of all the above collections is deposited in the Bishop Museum.

One collection, from a rather dry ridge, proves to be the following previously described form of *G. terminalis* var. *ovata:*

GOULDIA TERMINALIS var. OVATA f. **obovata** Fosberg, f. nov. Arbor glabra, ramulis angulatis; folia obovata coriacea; thyrsus hemisphaericus, pedunculis suberosis.

Tree up to 3 m. tall, branchlets strongly angled, internodes 0.5–2 cm. long, mostly about 1 cm., branches appearing dichotomous through the death of terminal inflorescences and development of a pair of branches from the basal node; leaves obovate, up to 6 cm. long and 3 cm. wide, coriaceous, apex obtuse to rounded, base strongly and abruptly contracted, obtuse to rounded, margin revolute, petiole up to 1 cm. long, about 1 mm. thick; stipules strongly carinate; thyrse hemisperical, up to 4 cm. long and 3 cm. wide, peduncle corky in fruit; flowers not known; fruit less fleshy than usual in this genus.

HAWAIIAN ISLANDS: LANAI: ridge below Puu Aalii, between Maunalei and Hauula drainages, rather dry forest, alt. 800 m., Nov. 30, 1935, ***Fosberg 12472*** (USNA—TYPE, BISH).

Differs from f. *euovata* in the smaller, plane, broadly obovate leaves, rounded or obtuse at both ends. This form extends the distribution of var. *ovata* to Lanai, where it seems logical that it should be found.

GOULDIA TERMINALIS var. OVATA f. SANTALIFOLIA Fosberg. Material collected by *Degener*, no. *12522b* (D, USNA), from southeast ridge of Iao Valley, west MAUI, HAWAIIAN ISLANDS, gives this form a somewhat broader distribution than known formerly. Heretofore, on Maui it has only been found in Olowalu Valley. The leaves of this collection are somewhat broader than is usual in this form, and not folded.

Degener's no. *12522* contained two sheets of f. *santalifolia*, several sheets of *G. terminalis* var. *cordata* f. *eucordata*, and a considerable number of sheets of a form that seems to be a hybrid between them. The latter is so distinctive in appearance that, had not the two presumed parents been present, I should probably have described it as a new form of var. *ovata*. It is glabrous, with angled long branchlets as in var. *cordata*, oblong to elliptic leaves and small spherical thyrses as in f. *santalifolia*, these appearing very compact. The node at the base of the thyrse, in many specimens, gives rise to two leafy branches, a character not common in the parents but suggesting var. *pseudodichotoma* of Lanai.

GOULDIA TERMINALIS var. PARVULA f. **impressa** Fosberg, f. nov. Arbor, ramulis non valde condensatis; folia oblonga vel obovata, obtusa, subtus pilosa.

Tree 15 feet tall, trunk 8 inches thick, branchlets strongly hirtellous, not strongly reduced, internodes 5–10 mm. long even in terminal portions; leaves oblong to obovate, up to 3.5 (rarely 5) cm. long, 2 (rarely 2.5) cm. wide, usually about half that size, obtuse or rounded at both ends, blade conspicuously pilose beneath, veins strongly impressed above, petiole 2–5 mm. long, glabrous.

HAWAIIAN ISLANDS: MAUI (east): Paliku, Haleakala, Aug. 5, 1939, *Degener 12521* (D—TYPE).

This form seems intermediate between f. *euparvifolia* and f. *subpilosa*, having the abundant pubescence and smaller leaves of the former, and the open habit of the latter, and differs from both in having both the apex and base of the leaves obtuse or rounded.

GOULDIA TERMINALIS var. PUBESCENS × var. PARVIFOLIA f. IMPRESSA. Like f. *impressa* but branchlets pubescent, internodes more elongate, leaves larger, more pubescent beneath.

HAWAIIAN ISLANDS: MAUI (east): Paliku, Haleakala, *Degener 12526* (D, USNA).

This is probably the correct disposition of this collection. The petioles are a trifle long for either parent. Perhaps a form of var. *ovata* may be involved, but none is known from this vicinity. Satisfactory disposal of the Gouldias from Maui awaits an opportunity for a careful field survey and extensive collecting.

GOULDIA TERMINALIS var. KAPUAENSIS f. **violetae** Fosberg, f. nov. Ramuli rigidi teretes, minute hirtelli; folia oblanceolata vel anguste elliptica, obtusa vel acuta, coriacea, subtus hirtella; thyrsus hirtellus; hypanthium hirtellum.

Shrub 1.5 m. tall, branchlets stiff almost to the tips, terete, minutely hirtellous; leaves oblanceolate to narrowly elliptical, up to 10 cm. long, 3 cm. wide, apex obtuse to subacute, coriaceous, hirtellous beneath, especially on the midrib, margin closely revolute, petiole up to 14 mm. long, about 1 mm. thick; thyrse about 2 cm. long, hirtellous; hypanthium somewhat hirtellous.

HAWAIIAN ISLANDS: HAWAII: Kau, between west and east arms of the 1907 flow, on dry lava, Aug. 10, 1936, *V. O. Fosberg 49* (BISH—TYPE).

Much like f. *pittosporoides* but very hairy and differing somewhat in leaf shape and slightly longer petiole. Named for the collector, Violet O. Fosberg.

GOULDIA TERMINALIS var. MACROCARPA f. CUNEATA Fosberg. Degener's collection cited below contains material with relatively large, somewhat obovate leaves 5–7 cm. long and 2.5–3.5 cm. wide, with the midribs hirtellous beneath, and also specimens with small oblong, somewhat revolute leaves, not so hirtellous, 3–4 cm. long, 1.5–2 cm. wide. These could scarcely have come from the same tree. The larger-leafed specimen corresponds well with f. *cuneata*, though the leaf bases are scarcely cuneate. This is a marked extension of the range of this form, known previously only from the plateau and western slope of the mountain of Kauai.

The small-leafed portion of this collection might be placed in f. *sclerophylla*, though the leaves are too thin and mostly too pubescent. It seems more likely, because of the restricted known distribution of f. *sclerophylla* and the discrepancies in leaf thickness and pubescence, that it is a hybrid between var. *macrocarpa* f. *cuneata* and var. *osteocarpa*, which latter is known to be widespread at low elevations on Kauai. The small-leafed plant is in flower while the large-leafed one has fruits which are enlarged because of insect attack.

HAWAIIAN ISLANDS: KAUAI: Kalualea, Koloa, alt. 1500 ft., *Degener & Ordonez 12645a* (large-leafed) and *12645b* (small-leafed) (D, USNA).

GOULDIA HILLEBRANDII var. NODOSA Fosberg. Two Degener specimens, collected near Mt. Eke, MAUI, HAWAIIAN ISLANDS, July 2, 1927, have the thyrses glabrous or almost so and seem in almost every other respect to fit var. *nodosa* rather than var. *typica*. One of them has the budding thyrses below the leaves, the other is in fruit. With the exception of the position of the inflorescences, a rather weak character, they match var. *nodosa* and may be regarded as extending the range of this variety to Maui.

Timonius kajewskii (Guill.) Fosberg, comb. nov. *Guettarda kajewskii* Guillaumin, Jour. Arnold Arb. **13**: 6. 1932.

This species, described from flowering material from the NEW HEBRIDES, Aneityum, *Kajewski 724* (A—TYPE, US), was known to its author in flower only. Another specimen, *Kajewski 826* (A, US), collected at the same locality, referred to *Guettarda* sp. by Guillaumin, is vegetatively identical, but bears peduncles with single fruits subtended by 2 vestigial bracts. The purple fruits are cylindrical, somewhat compressed, and with the apex prolonged to a point. They have the 12 cells sclerified, arranged in two parallel rows and fused into a ribbed stone. There seems little doubt that this plant is a fruiting specimen of Guillaumin's species, and that it should be referred to the genus *Timonius*, where its nearest relative is *T. smithii* Fosberg of Fiji (see Fosberg, Sargentia **1**: 121. 1942).

COPROSMA Forst.

Oliver's key (Bish. Mus. Bul. **132**: 28. 1935) separates *C. elliptica* from the *C. montana* group by the following contrast of characters:

Leaves with few secondary nerves, under 20 mm. long	*C. elliptica.*
Leaves penninerved; over 20 mm. long	Group of *C. montana.*

Although this will correctly separate the majority of specimens, my collections of *C. montana* var. *crassa*, nos. *9940* and *9977* (BISH), both from the upper part of Haleakala, MAUI, HAWAIIAN ISLANDS, and even a collection of *C. ochracea* var. *typica*, no. *10036* (BISH, USNA) from Puu Kukui, MAUI, have such small leaves and few nerves that they would go into *C. elliptica*, which they do not resemble. The following supplementary key will separate these small-leafed forms:

Ultimate branchlets 1–1.5 mm. thick	*C. elliptica.*
Ultimate branchlets 2 mm. or more thick, stiff.	
Pubescence short, inconspicuous	*C. montana* var. *crassa.*
Pubescence hirsute, dense	*C. ochracea* var. *typica.*

COPROSMA ELLIPTICA Oliver. A collection made in Alakai Swamp, KAUAI, HAWAIIAN ISLANDS, *Fosberg 12764* (BISH, USNA) has the pubescence much more sparse than, according to Oliver's description, the species ordinarily shows.

COPROSMA PUBENS var. TYPICA Oliver. This variety seems to be much more variable than Oliver's discussion (Bish. Mus. Bul. **128**: 171. 1935) would indicate. Of a series of collections from the Haiku Uka Trail, Makawao Dist., MAUI, *Fosberg 9847* (BISH, USNA) has leaves with blades 35–60 mm. long, fruiting peduncles up to 20 mm. long, bearing either 1 or 3 clusters of orange colored fruits; *Fosberg 9881* (BISH, USNA) has even smaller leaves, and peduncles tending to be slightly compound, fruits globose, 5–6

mm. across, orange; *Fosberg 9851* (BISH, USNA) has peduncles up to 30 mm. long, rarely compound, when simple having an articulation part way up bearing a small stipular sheath.

COPROSMA LONGIFOLIA Gray var. **longifolia** (Gray) Fosberg, nom. nov. *Coprosma longifolia* Gray, Proc. Am. Acad. **4**: 48. 1860.

This is the typical element of the species as described by Gray and restricted by Oliver (Bish. Mus. Bull. **132**: 177–179. 1935). It is common in the wetter regions of both mountain ranges on OAHU.

COPROSMA LONGIFOLIA Gray var. **oppositifolia** Fosberg, var. nov. Folia opposita, flos staminatus tubo corollae exserto lobis subaequalis 2–3 mm. longis, antheribus 4 mm. longis.

Leaves opposite, elliptic-lanceolate; stipular sheath 3–5 mm. long, appressed-hirtellous near base, with lobes 2–4 mm. long, somewhat acuminate, ciliate, glandular-denticulate; peduncle of staminate inflorescence 3–5 mm. long, bracts elliptic or ovate, corolla of staminate flowers funnelform, tube definitely exserted, strongly contracted below the expanded throat, tube plus throat 5–6 mm. long, lobes 6, subequal, 2–3 mm. long, bluntly lanceolate; anthers 6–8, linear-oblong, apiculate, lobed at base, 4 mm. long; pistillate flowers and fruit unavailable.

HAWAIIAN ISLANDS: OAHU: Waianae Mts., Makaha-Waianae Kai, Puu Kawiwi-Puu Kaala ridge, in wet forest, alt. 1150 m., March 31, 1935, *Fosberg 10855* (USNA—TYPE, Bish, A, F).

This variety differs most conspicuously from var. *longifolia* in its opposite leaves, definitely exserted corolla tube, much longer corolla throat and shorter peduncle and stipular sheath. From the other opposite leafed member of this group, *C. molokaiensis* St. John, this variety differs in its longer peduncles, the equally 6-lobed, rather than bilabiate, corollas, and shorter anthers. The slightly hirtellous stipules suggest a possibility of hybridization between *C. longifolia* and *C. ochracea* var. *kaalae*, recalling Oliver's suggestion (Bish. Mus. Bull. **132**: 175. 1935) for *C. molokaiensis*. The evidence at hand does not justify a suggestion of such an origin for this variety, but the presence of the two possible parents in the vicinity of the type locality gives reason to look into the matter at some future time.

BORRERIA LEAVIS (Lam.) Griseb. This weed, which is now widespread in the tropical Pacific, is becoming common in the Hawaiian Islands. It is a low plant with pectinate stipules and terminal and axillary densely capitate verticels of small white or pinkish flowers. The fruits are 2-celled capsules, both cells of which are ventrally and apically dehiscent, leaving a sub-persistent septum. In each cell is a single oblong, brown, transversely rugulose seed.

HAWAIIAN ISLANDS: OAHU: Maunawili, Kailua, *Fosberg, Storey, & Oliveira 10772* (BISH, USNA); Woodlawn, Manoa, Honolulu, *Fosberg 14111* (BISH, USNA); Manoa Valley, Honolulu, *Fosberg 10587* (BISH); University Campus, Manoa, Honolulu, *Fosberg 10528* (BISH, USNA).

RICHARDIA BRASILIENSIS (Moq.) Gomez. The plant common in the Hawaiian Islands which is usually referred to *Richardia scabra* L. or *Richardsonia scabra* (L.) St. Hil. really belongs to *R. brasiliensis*. This species was mentioned as occurring in the Hawaiian Islands by Schumann (in Engler & Prantl, Die Nat. Pflanzenf. IV, **4**: 139. 1891). Examination of

fruits of the common Hawaiian weed shows that the nutlets have the ventral face excavated and the general outline heart-shaped. *R. scabra* has cylindrical fruits with an almost closed ventral groove.

HAWAIIAN ISLANDS: KAUAI: Milolii Ridge, Waimea, alt. 2000 ft., *St. John, Fosberg & Oliveira 13739* (BISH, USNA).

COMPOSITAE

ELEPHANTOPUS MOLLIS HBK. According to Dr. S. F. Blake, the plant from Kauai referred to *E. tomentosus* in my paper of 1937 (Occ. Pap. Univ. Haw. 32: 9, 1937) really belongs to *E. mollis*, a native of tropical America that is widespread in tropical regions as a weed.

PSEUDELEPHANTOPUS SPICATUS (Juss.) Rohr. The plant called in the same paper *Elephantopus spicatus* Juss. is, according to Dr. Blake, better regarded as belonging to the genus *Pseudelephantopus*, distinguished by the spicate arrangement of the heads and the peculiarly curved, rather than straight, lateral pappus awns.

AGERATUM HOUSTONIANUM Mill. This garden plant was twice collected growing spontaneously near Honolulu. It may be distinguished from the common *A. conyzoides* L. by its larger heads and lance-linear, densely hairy, rather than oblong, sparingly hairy or glabrous involucral bracts.

HAWAIIAN ISLANDS: OAHU: Nuuanu Valley, June 6, 1937, *Fosberg 14004* (BISH); Manoa Valley, Woodlawn, May 22, 1937, *Fosberg 13835* (BISH); Honolulu, cultivated, *Fosberg 9368* (BISH).

SOLIDAGO ALTISSIMA L. The golden-rod which has escaped from gardens in Nuuanu and Manoa Valleys, Honolulu, has been identified by Dr. S. F. Blake as this species.

HAWAIIAN ISLANDS: OAHU: Honolulu, Nuuanu Valley, Dowsett Tract, Oct. 10, 1936, *Fosberg 13294* (BISH, USNA).

Dubautia sherffiana Fosberg, sp. nov. Frutex ad 0.5 m. altus; foliis alternis, elliptico-lanceolatis; paniculis corymbosis congestis glandulo-pubescentibus; capitulis 6–7 mm. altis, floribus 3–4 exsertis 5-meris, achenis subglabris prismaticis 2.5–3 mm. longis valde costatis, ad basin angustatis.

Shrub 0.5 m. tall, branchlets cylindric, gray, hispidulous, with alternate leaves 4 mm. or less apart, persistent only in the upper 10 cm. of the branchlet; leaves elliptic-lanceolate, 6–7 cm. long, 1–1.5 cm. wide, acute at apex and base, coriaceous, subsessile, appearing glabrous but minutely scabrous on margins, slightly so on under surface, becoming hispidulous toward base, margins somewhat revolute, remotely serrulate in distal half, at broadest part obscurely 11-nerved, nerves occasionally anastomosing to form an irregular and incomplete longitudinal reticulation, the petioliform base appressed to stem for about 2 mm.; inflorescence a crowded terminal corymbose panicle rounded or flattish on top, densely spreading-pubescent and with sparse short gland-tipped hairs, the rhachis up to 5 cm. long, terminating in perfect specimens in a reduced head, or this lacking, panicle branches up to 6–7 cm. long, scattered on the rhachis, subtended by leafy bracts similar to the leaves but greatly reduced, secondary branches subtended by still smaller bracts, on these branches the sessile heads glomerate at the apices, with a few scattered ones further down or with several very small branches

ending in small glomerules, each head closely subtended by a small densely ciliate somewhat ventricose bract; glomerules mostly with 3–6 heads, these 6–7 mm. high, about 2–3 mm. wide above, with 3–4 strongly exserted florets; involucre of 3–4 coherent or slightly connate bracts, narrowly cylindric-campanulate, 3–4 mm. high, 1–1.5 mm. thick at apex, often splitting with the development of the achenes, externally glandular, the free tips densely ciliate, involucral bracts cuneate, the low triangular free portion usually with 1 or 2 small lateral teeth; corolla apparently yellowish-white, 5-lobed, tube about 1–1.2 mm. long, throat abruptly enlarged and campanulate near middle, about 1.7–2 mm. long, lobes ovate, strongly recurved, at least in age, 1–1.3 mm. long; anther tube straw-colored, about 1.3 mm. long, partly or completely exserted, the terminal appendages ovate; achenes prismatic, 2.5–3 mm. long, 0.5–0.6 mm. thick at apex, tapering to base, about 8-ribbed (some ribs very prominent, others less so, sometimes 1 or 2 obscure), dark gray, very sparsely pilosulose toward apex, surface slightly roughened; pappus of a single series of about 25 plumose aristae 2.5–3 mm. long, united at extreme base, brownish-white.

HAWAIIAN ISLANDS: OAHU: Waianae Mts., brushy ridge east of 2nd gulch east of Kaupakuhale, Mokuleia, Oct. 23, 1932, *St. John & Fosberg 12161* (USNA—TYPE). "Great Crater, Hawaii," *U. S. Exploring Expedition* (US) (part, vide infra).

Named for Dr. E. E. Sherff of Chicago, monographer of *Dubautia* and *Railliardia*.

This species is so abundantly distinct that it is difficult to relate it to any particular known species. It belongs with the group called by Gray, and later by Sherff, section *Nervosae* of the genus *Railliardia*, which genus has been reduced to *Dubautia* by Keck (Occ. Pap. Bish. Mus. **11**: (19) : 24–28. 1936). In Sherff's treatment of *Railliardia* (Bish. Mus. Bull. 135: 106–136. 1935) *D. sherffiana* keys nearest *R. lonchophylla* Sherff [*Dubautia lonchophylla* (Sherff) Keck], which it does not resemble, or to *R. reticulata* Sherff [*Dubautia reticulata* (Sherff) Keck], but differs from the latter in having alternate subglabrous leaves, instead of opposite white-hispid ones, sessile, much shorter, fewer-flowered heads, practically glabrous instead of white-hispid achenes, and other less important characters. *D. reticulata* is known only from Maui.

Sherff credits only two species of *Railliardia* to Oahu—*R. scabra* [*Dubautia scabra*] of which I can find no citation of a specimen and *R. linearis* [*D. linearis*] of which one U. S. Exploring Expedition collection from Kaala is cited. Of these, *D. linearis* comes closest to *D. sherffiana* but differs in having its leaves narrower, only 3- to 5-nerved, and ternate instead of alternate; heads usually pedicellate instead of sessile, with 4–8 florets instead of 3–4 and pubescent involucres. Although Sherff says that the florets of *R. linearis* are included, examination of all of the material in the U. S. National Herbarium shows that they become quite well exserted when reasonably mature. In small size the heads of *D. sherffiana* are approached only by those of *D. linearis*, and this may probably be its closest relative, though this is by no means a final decision. I have not seen the Oahu specimens of *D. linearis* cited by Sherff, but assume that they are correctly placed. On one sheet of the U. S. Exploring Expedition material (US) said to be from "Great Crater, Hawaii" are 2 twigs. One is typical *D. linearis*, while the other has alternate,

much larger, 7-nerved lanceolate leaves, and mostly sessile, only slightly puberulent involucres. It undoubtedly belongs in *D. sherffiana*, and may well have come from Oahu, as the localities on the U. S. Exploring Expedition specimens were often woefully confused.

CHRISTMAS ISLAND

A number of species may be added to the known flora of Christmas Island on the basis of my collections made there in August 1936. The following are not in Christophersen's annotated list (Bish. Mus. Bull. 44: 22–27, 1927). All except *Abutilon indicum* and possibly *Portulaca fosbergii* appear to be introduced.

CYPERUS ROTUNDUS L. A small colony in the village, London, *Fosberg 13282* (BISH).

PORTULACA FOSBERGII Von Poelln. Paris, *Fosberg 13269* (BISH, USNA) (det. H. St. John). This species seems intermediate between *P. oleracea* L. and *P. lutea* Sol. Further study of living material is needed to determine its position in relation to these two species.

LEUCAENA GLAUCA (L.) Benth. London, *Fosberg 12171, 13249* (BISH).

PHASEOLUS LATHYROIDES L. Paris, *Fosberg 13269* (BISH, USNA).

ABUTILON INDICUM Sweet. This shrub forms a conspicuous part of the vegetation near Four Brothers, *Fosberg 13215* (BISH, USNA). The species has previously been reported only from Jarvis and Baker Islands in the central Pacific. It is common in tropical Asia.

HIBISCUS TILIACEUS L. Paris, *Fosberg 13267* (BISH). Probably planted.

FALLS CHURCH, VIRGINIA

BULLETIN OF THE TORREY BOTANICAL CLUB
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ANOTHER DRIFTLESS AREA ENDEMIC

NORMAN C. FASSETT

COMMELINA ERECTA L. var. **Greenei** Fassett, var. nov., foliis 10–15 cm. longis 6–8 mm. latis; spatheis maturis 1.5–2.7 cm. longis basi longe albido-villosis. WISCONSIN: on sand derived from crumbling sandstone, Cactus Bluff, 5 miles southwest of Sauk City, Sauk County, August 27, 1940, *J. T. Curtis & H. C. Greene* (TYPE in Herb. Univ. of Wisconsin); same station, July 7, 1941, *L. H. Shinners 3993;* same station, September 28, 1942, *N. C. Fassett & H. C. Greene 22056.*

This Driftless Area endemic (see Fassett, Rhodora **33**: 227, 228. 1931) has the size and proportions of var. *Deamiana* (Fernald, Rhodora **42**: 435–441. 1940) but differs in having long jointed white hairs on the spathe. Thus it bears the same morphological relation to var. *Deamiana* that f. *intercursa* Fernald does to var. *typica*, and that f. *crispa* (Wooton) Fernald does to var. *angustifolia* (Michx.) Fernald. It may, therefore, seem illogical to treat it as a variety when its counterparts are treated (and rightly) as forms. The reason is that while f. *intercursa* occurs as a sporadic variation throughout the range of var. *typica*, and f. *crispa* in like manner throughout the range of var. *angustifolia*, var. *Greenei* occupies a different area from that occupied by var. *Deamiana*. The latter occurs primarily in a limited range in northern Indiana[1] and northern Illinois, and has spathes always lacking white hairs more than 1 mm. long, as is evidenced by Fernald's statement based on his examination of the 16 collections cited by him, and corroborated by my own examination of the 16 sheets of this variety in the Deam Herbarium and the 6 in the Herbarium of the University of Wisconsin. That the plant of Cactus Bluff, isolated by some 200 miles from var. *Deamiana*, consistently has white-villous spathes is indicated by study of the 3 collections cited above; the last consists of 8 fruiting tops (all that could be found) collected for the purpose of studying the colony as a whole rather than a few individuals taken at random.

Var. *Greenei* occurs in very small numbers; Dr. Greene and I were able to find only 8 individuals. Such occurrence of rarities in extremely small numbers is quite characteristic of this part of Sauk County, which lies just within the Driftless Area. Only a few rods from the *Commelina*, on the steep face of Cactus Bluff, are a few individuals of *Pellaea atropurpurea*, known elsewhere in Wisconsin from two other bluffs, one a mile away and

[1] Mr. Deam has kindly loaned me his material of this group; the *C. angustifolia* of his Flora of Indiana (see pp. 285, 286, and Map 592) breaks clearly, in light of Fernald's treatment, into *C. erecta* var. *typica* in southern Indiana and var. *Deamiana* in northwestern Indiana.

the other 10 miles to the northwest. *P. atropurpurea*, primarily a southern plant isolated in the Driftless Area, occurs only in very small numbers, but *P. glabella* (Butters, Am. Fern Jour. **7**: 77–87. 1917), its common northern relative, is on nearly every cliff in southern Wisconsin (Tryon *et al.* The ferns and fern allies of Wisconsin, 23, 24. 1940). Mill Bluff, a mile and a half north of Cactus Bluff, was the type station for *Aconitum noveboracense* var. *quasiciliatum* (Fassett, Rhodora **31**: 49. 1929), where a very few individuals were seen (it is likely that it is extinct there now, since the woods shading the bluff have been cut). Fifteen miles to the northeast is Parfrey's Glen, where probably not more than a dozen individuals of the *Aconitum* cling to the moist shady walls of a ravine. Thirty miles northward, at Wisconsin Dells, *Rhododendron lapponicum* grows on cliffs along the Wisconsin River, at the only known station west of the Adirondack Mountains and south of Hudson Bay; it is doubtful if there are a score of individual plants at this place and their existence is menaced by the fact that the cliff on whose edge they grow is being cut back by the river faster than the newly exposed surfaces can be recolonized.

Surely many of the specialties of the Driftless Area are on the very brink of extinction.

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SUPPLEMENTARY NOTES ON AMERICAN MENISPERMACEAE—III

B. A. KRUKOFF AND H. N. MOLDENKE

New collections of the Menispermaceae, largely from Amazonian Brazil and Surinam, have recently become available to us. The Amazonian specimens were largely obtained in the municipality São Gabriel, State of Amazonas, on the tributaries of the upper Rio Negro, which are poorly known (to say the least) botanically. The collections were found to be of considerable interest and are discussed in the present paper. They extend our knowledge of certain species previously known from incomplete material; extensions of ranges are noted for a number of species, and three species are described as new. No changes in the nomenclature are necessitated.

The species are arranged in the same order and the place of deposit of specimens is shown by the same abbreviations as in our previous papers (1, 2, 3, 4). The following new abbreviation is used:

U: Georgetown Botanic Gardens at Georgetown, British Guiana.

CHONDODENDRON RUÍZ & PAVON

2. CHONDODENDRON PLATIPHYLLUM (A. St. Hil.) Miers. *Additional specimens examined: photos #34502* and *34501.*

As is evident from the labels (*photo #34502*), two specimens appear to be mounted on a single sheet, one collected by Casaretto in virgin forest in the State of Minas Geraes, and another collected by Richard near Rio de Janeiro.

Without seeing the actual specimen we are unable to ascertain whether or not *photo #34501* is of the type of *Cocculus ? cinerascens* A. St. Hil. The specimen was collected by Saint-Hilaire in forests near Rio de Janeiro.

3. CHONDODENDRON TOMENTOSUM Ruíz & Pav. *Additional specimens examined:* Peru, Ecuador, or Brazil, *collector undesignated 3, 10.* ECUADOR—NAPO-PASTAZA: basin of Rio Pastaza, *Gill 12363/6.*

On the labels of *collector undesignated 3* and *10* it is stated: "collected by Squibb's collector somewhere in Amazonian South America. Said to be a constituent of curare arrow-poison."

4. CHONDODENDRON CANDICANS (L. C. Rich.) Sandw. *Additional specimens examined:* BRITISH GUIANA—ESSEQUIBO: basin of Issororo River, *Jenman 5199* (U). Surinam—near Sectie O, on railroad Paramaribo-Dam, *Krukoff 12305, 12335.*

It is satisfactory to have new collections of this species from Surinam. The species was known to us from Surinam only from the type collection of *Abuta ? Pullei.*

5. CHONDODENDRON LIMACIFOLIUM (Diels) Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12090, 12092, 12093, 12095.*

7. CHONDODENDRON TOXICOFERUM (Wedd.) Krukoff & Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *? Froes 12087.*

SCIADOTENIA MIERS

3. SCIADOTENIA SOLIMOESANA Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS, basin of the upper Solimoes, *Froes 12094.*

This is the third collection of the species known to us.

ANOMOSPERMUM MIERS

1. ANOMOSPERMUM SCHOMBURGKII Miers. *Additional specimens examined:* BRITISH GUIANA—ESSEQUIBO: *Jenman 1333* (U); basin of Mazaruni River, *Jenman 2454* (U); Berbice: basin of Corentyne River, *Jenman 102* (U).

2. ANOMOSPERMUM DIELSIANUM Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12467.*

This is the first record of the species from the basin of Rio Negro (Corocoro on Rio Vaupes). It has been known hitherto only from the type collection from the basin of the upper Solimoes.

6. ANOMOSPERMUM CHLORANTHUM Diels. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12413.*

This is the first record of the species from the basin of Rio Negro (Yuco on Rio Xie). The specimens are more pubescent than any of the previously examined and cited material.

7. ANOMOSPERMUM sp. nov. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12151.*

In a previous paper (1) we have given a description of a plant which presumably has never previously been described or named, but have not assigned a specific name to it in view of lack of flowers or fruits. The present collection is again sterile and from the same region as the two previous collections.

8. ANOMOSPERMUM BOLIVIANUM Krukoff & Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12407.*

This sterile specimen matches very well the type collection of the species. It has been obtained in an old clearing on "terra firma" near Cucui.

9. **Anomospermum hirsutum** Krukoff & Moldenke, sp. nov. Frutex scandens; ramulis gracilibus dense hirsutis, pilis patentibus fulvis; petiolis gracilibus dense fulvo-hirsutis; laminis foliorum coriaceis late ellipticis argute acutis vel breviter acuminatis et saepe plusminus apiculatis integris subrevolutis, ad basim acutis indistincte 3-pli-nerviis, supra glabris nitidisque, subtus plusminus fulvo-hirsutis; costa venisque primariis secundariisque supra valde impressis, subtus argutiuscule prominentibus; reticulo venulorum copiosissimo perspicuo.

A woody vine; branchlets slender, densely hirsute on protected parts with spreading fulvous hairs 1–2 mm. long, less so or even glabrescent on the internodes; petioles slender, 2.5–3.8 cm. long, densely fulvous-hirsute, the uppermost 1 cm. swollen and usually more or less curved; leaf-blades coriaceous, uniformly bright-green on both surfaces or more shiny above, broadly elliptic, 7.5–16.5 cm. long, 2.5–6.8 cm. wide, sharply acute or short-acuminate and often more or less apiculate at apex, entire and slightly revolute along the margins in drying, acute at base, glabrous and shiny above, more or less fulvous-hirsute beneath, especially along the midrib and larger venation, indistinctly 3-pli-nerved from the base, the main pair of veins not very dissimilar to the 3 or 4 pairs of secondaries and confluent with them in many loops 6–8 mm. from the margins; midrib, principal veins, and secondaries rather deeply impressed above, sharply prominent beneath; the tertiaries prominulous in shallow grooves above, prominent beneath; veinlet reticulation very abundant and conspicuous under a hand-lens, fine, prominulous on both surfaces; only staminate flowers seen; pedicels subtended by 2 minute scale-like triangular-ovate to lanceolate bractlets, which are about 1 mm. long, carnose-thickened at base, acute at apex, hirsute on the back, and easily separable; sepals 6, imbricate, the 3 outer ones minute, resembling the bractlet, unequal, triangular-ovate, about 1.5 mm. long and 1 mm. wide, subacute at apex, sparsely hirsute dorsally and hirsute-ciliate on margins, carnose-thickened at base, easily separable, the 3 inner ones very much larger, broadly elliptic or suborbicular, narrowed and somewhat claw-like at base, rounded at apex, cucullate with inflexed margins, subequal, about 5 mm. long and 4 mm. wide, extremely carnose dorsally, glabrous, easily separable; petals 6, much smaller than the inner sepals, obpyramoid, about 2 mm. long and almost as wide, extremely carnose, the margins greatly inflexed, closely pressed together with the 6 stamens, forming a glabrous truncated "pseudodisk"; stamens 6, inflexed, when not extended equalling the petals and opposite them; filaments subterete or somewhat flattened, free, glabrous; anthers facing down and subhorizontal, dehiscing by short longitudinal slits; pistillate infructescences axillary, compound, to 9 cm. long, usually shorter than the subtending leaf, with about 3–12 fruiting-pedicels; peduncles obsolete; rachis slender, densely spreading fulvous-hirsute like the petioles and branchlets; bractlets linear, about 5 mm. long, densely fulvous-hirsute, one subtending each pedicel; pedicels slender, 1.3–1.8 cm. long, sparsely hirsute, 1–3-fruited, expanded-capitate at apex; mature fruits asymmetric, about 2.8 cm. long and 1.2–1.4 cm. wide, the exocarp slightly fleshy, glabrous, shiny, wrinkled in drying; mesocarp thin; endocarp hard and bony, smooth outside, elevated-reticulate within.

TYPE: *Ducke 753* (N), collected June 14, 1941, near "Manaos, Estrada do Paredão, silva secundaria non inundabili."

The species is unique and is immediately distinguished from all other known species of the genus *Anomospermum* as well as of the genera *Abuta, Chondodendron, Elissarrhena* and *Telitoxicum* by its hirsute leaves.

Specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, *Ducke 753* (N, type); *Froes 12408*.

TELITOXICUM MOLDENKE

3. TELITOXICUM INOPINATUM Moldenke. *Additional specimens examined:* BRITISH GUIANA—BERBICE: basin of Eberoabo River, *Hohenkirk 55* (U—iso-

type); Weruni-Ituni Savannahs, *Abraham 132* (U); basin of Courantyne River, *Hohenkirk 714* (U).

ABUTA BARRÈRE

2. ABUTA OBOVATA Diels. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of Rio Negro, *Froes 12379, 12543, 12563.*

The species is now known both from the upper and the lower Rio Negro.

6. ABUTA PANURENSIS Eichl. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12414.*

The species has been known hitherto only from the type collection. The present collection is from "restinga" near Yuco on Rio Xie, municipality São Gabriel.

8. ABUTA IMENE (Mart.) Eichl. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12156;* basin of the upper Rio Negro, *Froes 12477.*

11. ABUTA GRANDIFOLIA (Mart.) Sandw. *Additional specimens examined:* VENEZUELA—AMAZONAS: basin of Rio Negro, *Froes 12387; Ducke 691.* BRAZIL—AMAZONAS: basin of Rio Tonantins, *Froes 12164, 12232.* SURINAM: near Sectie O, on railroad Paramaribo-Dam, *Krukoff 12296, 12324.*

This is the first record of the species from the basin of Rio Tonantins.

14. ABUTA RUFESCENS Aubl. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12088, 12089, 12091;* basin of Rio Negro, *Ducke 861.* FRENCH GUIANA: *Aublet s.n.* (? type; photo #34499).

The Brazilian specimens are the first record of the species from the basin of Rio Solimoes.

15. ABUTA BARBATA Miers. *Additional specimens examined:* SURINAM: near Sectie O, on railroad Paramaribo-Dam, *Krukoff 12325.*

16. ABUTA GRISEBACHII Triana & Planch. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the Rio Negro, *Froes 12434; Ducke 822.*

20. **Abuta negroënsis** Krukoff & Moldenke, sp. nov. Frutex scandens; ramis crassiusculis adpresso-pubescentibus vel glabrescentibus; ramulis gracilibus densissime velutino-pubescentibus, pilis brevibus brunneis; cicatricibus perelevatis; petiolis crassis firmis ad basim ampliatis, dense velutino-pubescentibus; laminis foliorum coriaceis ovatis acuminatis integris, ad basim acutis vel paullo obtuseque subacuminatis, supra glabris nitidisque, subtus dense velutino-tomentosis, pinnato-venosis.

A woody vine; branches rather stout, about 1.5 cm. in diameter, appressed-pubescent or glabrescent in age; branchlets slender, very densely velutinous-pubescent with short brown hairs; leaf-scars large and corky, very prominently elevated on sterigmata about 5 mm. long; petioles stout, firm, 13–24 cm. long, ampliate at base, thickened and curvate for the upper 1.5–2 cm., densely velutinous-pubescent like the branchlets, the pubescence eventually wearing off; leaf-blades coriaceous, ovate, 25–37 cm. long, 14.5–20 cm. wide, acuminate at apex, entire, acute or very slightly obtuse-acuminate at base, glabrous and shiny above, densely velutinous-tomentose beneath with short, appressed, brownish hairs, pinnately veined; midrib stout, im-

pressed and often appressed-pubescent above, very prominent beneath; secondaries slender, 8–10 per side, regularly ascending, arcuate near the margins, usually not plainly anastomosing, impressed above, very prominent beneath; tertiaries slender, numerous, joining the secondaries, issuing at right angles, subparallel, slightly impressed above, prominent beneath; veinlet reticulation abundant and regular, forming very fine meshes visible under a hand-lens; flowers and fruit not known.

TYPE: *Froes 12423* (N), collected Dec. 19, 1941, near Santa Ana, on Rio Içana, basin of the upper Rio Negro, State of Amazonas, Brazil.

The species is unique and is immediately distinguished from all other known species of the genera *Chondodendron*, *Sciadotenia*, *Anomospermum*, *Abuta*, *Elissarrhena*, and *Telitoxicum* by the combination of the following characters: leaf-blades woolly beneath and distinctly pinnate-veined (not pli-nerved!). The only other known species of American menispermaceous plants which have the leaf-blades woolly beneath are *Abuta Grisebachii*, *Abuta Candollii*, *Abuta splendida*, *Sciadotenia paraënsis*, *Sciadotenia Sagotiana*, and species of *Chondodendron*, and leaves of all of these are pli-nerved.

All known species of *Chondodendron* are characterized by the matted indumentum whereas the leaves in our species are tomentose. Because of the absence of flowers, we cannot suggest its immediate relatives. It seems best placed in the genus *Abuta*.

21. **Abuta Froesii** Krukoff & Moldenke, sp. nov. Frutex scandens; ramis ramulisque gracilibus glabris nitidis; cicatricibus magnis elevatis circularibus suberosis; petiolis gracillimis glabris; laminis foliorum firme chartaceis ellipticis integris, ad apiceum rotundatis et cuspidato-acuminatis, ad basim rotundatis vel acutis, utrinque glabris pernitidisque, 5-pli-nerviis.

A woody vine; branches and branchlets slender, glabrous, shiny; lenticels usually prominent; leaf-scars large and elevated, corky, circular; petioles very slender, 2.5–7 cm. long, glabrous, somewhat ampliate at base, the uppermost 5 mm. thickened and curved; leaf-blades firmly chartaceous, uniformly colored on both surfaces, elliptic, 5.5–15.5 cm. long, 3–8 cm. wide, rounded to a short cuspidate-acuminate apex, entire, rounded or acute at base, glabrous and very shiny on both surfaces, 5-pli-nerved from the base; midrib and primary veins very slender, plane above, sharply prominent beneath; the lower pair of primary veins not as prominent as the upper pair, closely paralleling the leaf-margin half way to its apex, the upper pair not very arcuate, ascending almost to the apex, not anastomosing with the other pair nor with the secondaries; secondaries 1 or 2 pairs, in the upper half of the leaf, arcuately looped, not reaching the margins, anastomosing; tertiaries and veinlet reticulation obscure above, only the larger portions subprominulous beneath; flowers not seen; pistillate infructescences supraaxillary; peduncles stout, about 1 cm. long, subglabrous, surmounted by a large club-like receptacle, bearing (normally) three fruits; fruit asymmetric, 3–3.5 cm. long, 2–2.5 cm. wide, glabrous; exocarp hard and bony; mesocarp woody; endocarp thin, smooth and shiny, not corrugated.

TYPE: *Froes 12346* (N), collected Jan. 31, 1942, on "terra firma" near Macubeta on Rio Marie, basin of the upper Rio Negro.

The species resembles *Abuta brevifolia* from which it differs, however,

in its much larger fruits with the glabrous exocarp, much longer petioles, and larger leaves.

Specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, *Froes 12436;* basin of Rio Solimoes, *Froes 12168, 12180.*

ELISSARRHENA MIERS

1. ELISSARRHENA GRANDIFOLIA (Eichl.) Diels. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12084.*

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WHAT IS THE TRINOMIAL TYPICUS?—II

LEON CROIZAT

The reader who has so far followed this discussion is aware by now of the sad plight of much nomenclature in our midst, and knows a few of the disruptive interpretations and peculiar ideas bearing upon the typic trinomial. This reader will agree, it may be believed, that a sane and constructive approach to the all-important problem of typification is impossible so long as the fundamentals in the issue are flouted, and the discussion wanders in a maze of pompous and ill-digested generalities. *Sharp and precise biological concepts such as necessarily underlie good classification cannot forever speak the language of fanciful nomenclature,* nor can the facts be concealed and disguised. It is no longer a question of names that are being published on occasion and prove untenable on account of some technical violation of the Rules, but of a whole deeply-rooted trend of unsound thought and haphazard practice, ultimately based on a lack of familiarity with the subject. The hair-splitting and the abuse of imagination which have characterized the work of some recent writers on nomenclature have damaged, no doubt, the cause of the serious student who is well aware that quibbling and wild hypothecating are as obnoxious in the long run as ignorance and neglect. At bottom, the Rules of Nomenclature are not a pack of cavil, the plaything of a few devotees, or the Book of Merlin. *They are a labor-saving device in the first place, making it possible for everybody to speak briefly and to the point on subjects of common interest.* Properly expounded, they are as easy to read and to understand as the rules governing any current card game. In a very definite sense, they must become a live reality to every botanist.

The fallacies surrounding the trinomial *typicus,* its nature and use, have no reason to exist, because this trinomial has nothing in it which is mysterious or difficult once its fundamentals are grasped. Rather than discuss these fundamentals in the abstract, I will deal with them by examples and plain considerations.

As an introduction, we may consider the following formula:

$$1 + x = 2;\ x = 2 - 1;\ x = 1.$$

Half a line of symbols and figures written in a matter of seconds speak an amount of truth which, put into words, would require considerable time and paper. The formula given above summarily states the following: A certain figure, conventionally designated by the symbol x, meaning a quantity unknown, when added to 1 yields 2. To find this figure transfer to the right of the symbol of equality the figure 1, changing its value from positive to negative, leaving x in its original position to the left of the sign of equality.

The result of the subtraction (2 – 1) eventually yields 1, which is the value of x.

Precisely like mathematics, botany speaks in symbols and formulae, witness this: *Hydriastele Kasesa* (Laut.) Burret, comb. nov. = *Ptychosperma Kasesa* Laut. in Engl. Bot. Jahrb. **45**: 357. 1911. By the use of this formula, Burret (Notizbl. Bot. Gart. Berlin **13**: 484. 1937) tells his coworkers the following: "In a periodical called Engler's Botanische Jahrbücher, Volume 45, page 357, printed in 1911, Lauterbach has validly and legitimately published a certain species which he has designated as *Ptychosperma Kasesa*. I, Burret, having investigated the creation of Lauterbach, found in it characters which assimilate it to the species in the genus *Hydriastele*. Accordingly, I have brought Lauterbach's species away from *Ptychosperma* under *Hydriastele*. This of course, is my own, Burret's, understanding of the matter."

Obviously, it may not be doubted that botany, too, is ruled by a special kind of symbolic and abbreviated language. Nomenclature is essentially that branch of botany which is concerned with the proper use of such a language. The usefulness and nobility of nomenclature cannot be disputed or denied, for without it the use of this expeditious language would be impossible. Without this language, Burret would have been obliged to state its story in detail, that is, would have been forced back to the polynomial stage of botany and possibly farther still, to the age of Theophrastus and Pliny.

Let us now suppose that a taxonomist, J. Brown, is faced with the task of writing down the following account: In 1900 J. Doe published as *Planta una* an entity with a glabrous body and blue flowers. In 1905, P. Smith found a pubescent annual with blue flowers which he judged to be conspecific with *P. una* and published it trinomially, either as a subspecies or as a variety, as *P. una pilosa*. Five years later, in 1910, C. Black collected a pubescent herb with white flowers which he proposed as a form, *P. una albiflora*. Lastly, in 1915, N. Toe collected a glabrous herb with white flowers which he published as a form calling it *P. una leucantha*.

Using the standard language of botany, J. Brown has a free choice between two manners of expressing this long-drawn account. He can do this:

Planta una J. Doe, 1900.

P. una f. *leucantha* N. Toe, 1915.

P. una (subsp., var.) *pilosa* P. Smith, 1905.
P. una f. *albiflora* C. Black, 1910;

or this:

Planta una J. Doe 1900

P. una (subsp., var.) *typica* J. Brown, 1942.
P. una f. *leucantha* N. Toe, 1915.

P. una (subsp., var.) *pilosa* P. Smith, 1905.
P. una f. *albiflora* C. Black, 1910.

It will readily be seen that, while the two accounts substantially agree in the facts they reveal, the latter is in every respect better balanced. The

species itself is conceived as a broad unit, including both kind of plants, glabrous and pubescent, of which the glabrous entity is considered to be typical in the nomenclatural if not in the biological sense. The form *leucantha* spoken of as *P. una* var. *typica* f. *leucantha* is immediately known to be glabrous, therefore to belong to a complex other than the form *albiflora*. The trinomial *typica* neatly balances the trinomial *pilosa*, and a comparison between the type-specimens of the two can be effected without calling into question a binomial (*P. una*) and a trinomial (*P. una pilosa*) which may engender confusion. In brief: the segregation of the trinomial *typicus* has nothing about it which is mysterious, involved and philosophical; it is merely a book-keeping device which has for its result to simplify and elucidate the treatment of involved and much subdivided entities. This device is sprung into action by the simple expedient of publishing a trinomial (subspecies, variety or form) which is based upon the same type-specimen as the next higher unit; *P. una* and *P. una* var. *typica* being both based upon *J. Doe 482*, a specimen collected—let us say—near Washington, D. C., in 1899.

Some workers who are not familiar with this elementary device believe that *P. una* and *P. una* var. *typica* are synonyms, because—they say—"both these names apply to the same plant." This is a patent fallacy; to be synonymous (see Art. 16) two names must have the same *circumscription* (that is, be based upon specimens of the same significance and value in classification[2]), *position* (that is, be both under the same genus, species, variety, and the like), and *rank* (that is, be both genera, species, subspecies, varieties, or the like). It is clear that *P. una* and *P. una* var. *typica* cannot be synonyms, because they are short of two out of three elements required for a synonymy; they have the same *circumscription*, true enough, because they are both

[2] The term *circumscription*, etymologically considered, means to "write in" or to "delineate around," and is used by botanists in two senses, as follows: (a) To refer to groups in general. Accordingly, we hear that, for instance, "Exceedingly narrow circumscriptions were understood by Rafinesque to form good genera." (b) To define the taxonomic range of a specimen, as it were, thus: "*J. Doe 415* and *T. Brown 11* are collections with the same circumscription." It will readily be seen that the etymology of the term itself is compatible with these two different uses, and that both, consequently, are correct. However, the Rules speak of *circumscription* in the second sense only in the text of Art. 16. Users of the Rules should be careful not to understand the language of the Articles in the sense which is often colloquially current. A classic example of the confusion that results from misunderstanding the Rules in this manner, is Wheeler's contention (Contr. Gray Herb. 127: 53. 1939) that Watson published *Bernardia* (!) *fasciculata* as a *nomen provisorium* because he said that this name was ". . . only provisionally referred to *Bernardia*." That this notion is fantastic can readily be seen, considering that if Wheeler were correct every name published with an expression of doubt as to its true position or ultimate destination would be invalid. A *nomen provisorium* in the sense of the Rules (see Croizat, Jour. Arnold Arbor. **21**: 499. 1940; **22**: 137. 1941; Bull. Torrey Club **69**: 454. 1942) is a very different thing. The rules must be read for what they are and must be used accordingly; no one should apply a monkey-wrench fitting the gear of a truck to the threads and screws of a fine microscope, for common sense forbids it.

based upon the very same specimen, but they do not have the same *position* (*P. una* stands under genus *Planta* while *P. una* var. *typica* stands under species *P. una*), nor the same *rank* (*P. una* is a species, *P. una* var. *typica* a variety).

The objection is sometimes heard that all these subtle distinctions among circumscriptions, positions, ranks and the like are quibbles, and that a botanist cannot be expected to waste his time nor to live by the codes of a lawyer. This objection must be buried once for all, for it sins against elementary reason. The difference between a competent and an incompetent worker is in the fact that the former has taken pains to learn to use all the instruments of his craft; meeting a difficulty, a straight-thinking student masters it once for all, and does not complain about it forever. The Treasury of the United States also makes some distinction between scraps of paper of the same size, texture and color, paying one-tenth as much for some of them, depending upon the fact that on these scraps the figure 1 is followed by one zero rather than by two. Strange to say, the supercilious and overbusy workers who dismiss circumscriptions, positions, and ranks with a sweeping and hopeless gesture of their hands are well informed of the "quibbles" of the Treasury, and never fail to exact their pound of flesh in good bills, squeezing the last drop of blood out of the Treasury's "legal notions." It is not very clear why these workers should dismiss as nonsense what the Rules of Nomenclature say, when, after all, they use taxonomic names fully as frequently as they do cash. True, profound treatises can be written about the conceptual background of x in mathematics, the theory of double entry in bookkeeping, the philosophy of the bad bridge player or of the shrewd "plunger" on the stock market, and about the nature of *typicus*. However, the average taxonomist has no need of all this literature to ply his trade well and intelligently. All that matters to him is to have a good grasp of the possibilities of the trinomial epithet *typicus* and of the brand of calisthenics which this epithet performs in actual use. It stands to reason that taxonomists who deal with complex entities or make a rigorous study of populations and variations need to use the trinomial *typicus*, and actually use it (see, for instance, St. John & Hosaka, Occ. Pap. Bishop Mus. **14**: 120. 1938; Clausen, Keck & Hiesey, Carnegie Inst. Wash. Publ. 520. 1940), while taxonomists who are fortunate enough to labor upon floras continuously yielding new species and possibly new genera have no feeling for this trinomial. The point is not that these are wise and those foolish, or the other way around. The point is, rather, that the practical necessities of the branch of taxonomy which these botanists serve call into play different means and methods, some playing the strings, others the brasses, in the orchestra of Flora. That all botanists should understand the needs of all botanists and be able on occasion to use all their tools is to be believed as a matter of course. It is none the less plain that since *typicus*

is meant to simplify, not to complicate matters, those who whip it into a froth of decorative generalities and ill-digested abstractions do not follow the middle of the road where alone common sense dwells.

A fallacy commonly heard about *typicus* is that this trinomial is a "new name." To begin with, this is denied by the Rules, for whenever they speak of a "renaming" or of a "new name" (see, for instance, Art. 61 and Art. 69), they refer to entities of the same rank, that is, to a species' acquiring a "new name" because an old and untenable binomial falls out, because a generic illegitimate name is replaced by another generic tenable unitarian designation, and the like. The Rules know better than to speak of a trinomial being given a binomial as a "new name." The Rules know, as a matter of fact, that to confuse ranks means to open the door to such errors as have been illustrated in the preceding discussion of Art. 58 and Art. 30.

The fact that the trinomial *typicus* cannot be a "new name" is conveniently illustrated by examples, this one, for instance: Mueller Argoviensis published *Mallotus oreophilus* (in DC. Prodr. **15**(2): 964. 1866) without ending the specific description with the designation of a type-specimen. At the same time, however, he published two trinomials, α *ochraceo-albidus* and β *floccosus*, typifying the former by a specimen with whitish-tomentose, the latter by one with glabrescent leaves. Of these trinomials the former, designated by the letter α is the full equivalent of a trinomial *typicus* because its type-specimen is also the type-specimen of the binomial.

Translated into plain language, Mueller's publication means that he recognized an entity (the species, *M. oreophilus* in the broad sense) with general characters of fruit, flower and the like that applied in common to the subdivisions of this entity (the varieties, distinct in the nature of their indumentum at the leaf), one of these subdivisions being accepted by him as typic of the species as a whole *in the nomenclatural sense, not necessarily in the biological one*. It should not occur to a competent biologist and to a well informed taxonomist that the concepts involved in this treatment are two, for they are manifestly three, namely: (1) a broad aggregate of forms, whitish-pubescent to glabrescent in their foliage, but akin in the balance of their characters (*M. oreophilus*); (2) a subdivision of this aggregate with definitely whitish-pubescent leaves, this character in Mueller's opinion setting out a morphological and possibly a geographical complex (α *ochraceo-albidus*); (3) a subdivision like the preceding one but glabrescent in its foliage (β *floccosus*). Since the concepts here involved are three, not two, that bearing upon *M. oreophilus* in particular being unlike that of α *ochraceo-albidus*, it stands to reason that this trinomial cannot be, and is not a "new name" for the binomial. It is a *different name, for it applies to a different subject and holds within itself a different concept*. To designate *M. oreophilus* α *ochraceo-albidus* as a "new name" violence must be done to the whole

of the Rules which define as such something different. It is not clear in my understanding why such a violence should be done, when it leads only to ultimate confusion of terms and concepts, and serves no useful purpose at all. What does a taxonomist gain who follows the typic trinomial with the abbreviation "nom. nov." rather than with the accepted "var. nov." or "subsp. nov."? Does he affirm in so doing his faith in the esoteric side of nomenclature, proclaiming unto the ages his perfect understanding of the virtues of *typicus*? Indeed not: he merely states that his familiarity with the concepts underlying such a trinomial is less perfect than it ought to be, and confuses his coworkers by palming off as a "new name" of undefined status that which is clearly not so.

Some objection may be anticipated against my using in this summary two examples which are seemingly different without emphasizing this presumed difference. It may be pointed out that in the fancied case of *Planta una* J. Doe, 1900, the typic trinomial was segregated only in 1942 by a taxonomist other than J. Doe, namely J. Brown, while in the actual case of *Mallotus oreophilus*, Mueller himself immediately segregated the trinomial in question and a second one, failing to designate the type-specimen of the binomial.

No difference at all *in concepts* exist between these two examples. Proof of this is immediately had by comparing the examples I have used in their basic final form. Here they are:

(A) *Planta una* J. Doe, 1900.

P. una var. *typica* J. Brown, 1942. — *P. una* var. *pilosa* P. Smith, 1905.

(B) *Mallotus oreophilus* Muell.-Arg., 1866.

M. oreophilus var. *ochraceo-albidus* Muell.-Arg., 1866. — *M. oreophilus* var. *floccosus* Muell.-Arg., 1866.

Nothing would change in the realities involved by these citations if J. Doe himself had published var. *typica* in 1900, or if Mueller had waited half a century to announce var. *ochraceo-albidus*. Both *P. una* and *M. oreophilus* ultimately have acquired the conceptual status of the species in the broad sense, that is, of the biological complex as a whole. Their trinomials *typica* and *ochraceo-albidus* have exactly the same significance, that is, they stand for the part of the species broadly understood which is typic in the nomenclatural sense. Likewise, the subdivisions *pilosa* and *floccosus* are equivalent in this, that they represent a nomenclaturally atypic segment of the binomial. Clearly, the var. *typica* (1942) of *P. una* (1900) is no more a "new name" of the binomial than is the var. *ochraceo-albidus* (1866) of *M. oreophilus* (1866). Precisely in the same manner, two bars of iron of the same length and weight are identical regardless of the fact that one was sawed off the mother bar in 1866, the other in 1942.

The fallacies current on account of failure to properly understand the elements of time and concept in nomenclature are so numerous that I may add parenthetically a few words on the subject. As I have shown, Art. 18 pitilessly scrambles three "types," namely (1) type-names; (2) type-specimens; (3) biological types; falling as a result into the grossest contradiction. I have good reason to suspect that such unfortunate results are chargeable, more than to anything else, to a single factor. The near totality of taxonomists untrained in the use of *typicus* and trinomials in general overstress the element of time against the element of concept. Accordingly, they are panicky or rebellious when somebody speaks of the trinomial *typicus* as the "type" of the species. They cannot see this at all, for they point out that a species must have a "type," and that it is not true that all species have a trinomial *typicus*. Naturally, they argue, the "type" must be a specimen, figure, or description, for without such a "type" a species cannot even be born. A species, they further argue, does not need a trinomial *typicus* to be born.

Instead of turning obdurate or panicky, these taxonomists ought to consider that they can publish *Planta una* in two manners, (1) by designating the type-specimen and adding no trinomial, as follows: *Planta una*—type-specimen: *J. Doe 372.* (2) By designating the type-variety together with some other trinomial (in theory, the type-variety alone could be legitimately and validly published, nothing forbidding this in the Rules) and listing the specimen either after the binomial or after the typic trinomial, as follows: (a) *P. una*—type-specimen: *J. Doe 372;* var. *typica* (*una, genuina,* etc.); var. *lutea;* (b) *P. una;* var. *typica*—type-specimen: *J. Doe 372;* var. *lutea.*

It is for all to see that in the publication of *P. una* two elements are involved or may be involved, namely, (1) a type-specimen; (2) a type-variety. It is just as clear that the type-specimen may not be designated at publication, and so may not be indicated the type-variety. It is downright untrue, of course, that a species needs the designation of a type-specimen to be born. The species of older authors, as a matter of fact, were practically all published without mention of specimens, least of all of type-specimens. Naturally, it is just as feasible to publish a type-variety without designating a type-specimen, as it is to designate a type-specimen without publishing a type-variety. To elucidate this vital point, let us suppose that *Planta una* was published in 1801 in a valid and legitimate manner, without, however, the indication of a type-specimen or of a typic trinomial. It is open to a modern worker to choose right now this specimen and to publish this trinomial. Conversely, the type-specimen might have been chosen by a taxonomist in 1825 and the type-trinomial (var. *typicus, genuinus* and the like) published by another taxonomist in 1930. In other words: *the concept of type-specimen (or its equivalents, description and figure) and the concept*

of type-name (trinomial typicus or its equivalents) are both hidden within the entrails of the species at birth and no limitations in time exist—in principle—to their being pulled out to light. The taxonomists of an earlier generation were inclined to muster into the world the type-trinomial sooner than the type-specimen, thus publishing a var. *typica* or the like even before having designated the type-specimen; we moderns, on the contrary, not only incline to bring forth the type-specimen first, but go so far as to accept our point of view as the whole truth, denying that a typic trinomial and a type-name in general is a "type" at all. This is an error, and so long as this error lives we will be unable to progress in nomenclature, for nomenclature is the art of putting together right names and right specimens. Obviously, to fit these entities together well we should be able to effect at all times and under all circumstances the proper distinction, what is a name and what is a specimen. Somebody who was not innocent of nomenclatural affairs wrote in Rec. iv of the current Rules the statement that the type of a new name in a species is "the type-variety or specimen." Another somebody who was well advanced in knowledge, taking it for granted that sooner or later every species is bound to have a type-trinomial, spoke in Rec. xviii of the "subdivision of a species" which is "the type of the specific name." Since Art. 18, the ark in which is supposedly embalmed the "Type Method" itself, emphatically states that the type of a species is only a specimen, description or figure—as already pointed out—the reader may draw his own conclusions as to the happy state of affairs that now prevails, with two Recommendations which contradict a "fundamental" Article which contradicts itself.

Still another fallacy current on the score of *typicus* and its nomenclatural equivalents is the belief that these epithets have hidden virtues of their own, which set them apart from the common run of other taxonomic names. At the very end of the paper of Bolle elsewhere discussed in this review, Harms, Mattfeld, and Pilger contend that Bolle is wrong in his approach to the trinomial *typicus*, "da nach unserer Meinung diese Ausdrücke nach dem Sinne der Regeln nicht den eigentlichen Epitheta gleichzusetzen sind, vielmehr nur als Bezeichnungen fur eine Untergruppe gelten sollen, die dem Typus der übergeordneten Gruppe entspricht" (in our view, these terms—*typicus, genuinus,* etc.—cannot be assimilated to true epithets in the sense of the Rules, because they are mere symbols for subordinate units which contain the type of the higher ones).

On its face, this statement seems to be salted with philosophical flavor. Its authors draw a distinction between "Epitheta" and "Bezeichnungen," inferring that Bolle is at fault because he failed to perceive how substantially different are these two objects of nomenclatural thought, the "Epitheta" and the "Bezeichnungen." Had Bolle seen this radical difference, we are led to understand, he would not have written a paper at all to ask that

a Recommendation be enacted to check the spread of the use of *typicus, genuinus,* and the like trinomial epithets. Bolle would have worshipped the "Bezeichnungen" and the "Epitheta" at different shrines, as do his censors, and abstained from sacrilegious writing.

I do not believe that Bolle is right, as the reader knows, but I believe even less that his critics have a plausible case on their hands. The statement that *typicus* and its kindred are "Bezeichnungen" not "Epitheta" has mystical flavor much rather than philosophical taste. Like all mystical affirmations, this *pronunciamento* appeals to the heart of those who happen to accept it on faith, but cannot appeal to the mind of a dispassionate investigator. Once again, this is a saying which is rooted in something taken for granted rather than carefully digested. What amount of thought do I convey to myself and others when I utter the jaculatory: "The typic trinomial is not an epithet but a symbol (Bezeichnung)"? The answer is that I mean nothing at all. Every word, written or spoken, is both an epithet and a symbol of something that exists in nature or in the mind of man. Properly juggled, the letters a, e, r, t, and w spell *water* which is both the name (epithet) and the connotation (symbol) of a fluid that can be drank, swum through, and navigated on. So juggled, other letters can be made to spell *Cabralea macrantha* Harms, which is the name for a certain meliaceous plant from Rio de Janeiro, and the symbol of this entity in the eyes of a botanist, who by reading the name can visualize the plant. Still other letters suitably combined read *Croton scaber* Willd. var. *genuinus* Muell.-Arg., which is both the name and the "Bezeichnung" for a group under *C. scaber* which, being typic in the nomenclatural sense, if not in the biological one, cannot be segregated from *C. scaber.* Is there any difference between such a "Bezeichnung" as *C. macrantha* and such another as *C. scaber genuinus?* None indeed that can be seen; both apply to certain plants which they symbolize before the eye of a taxonomist. True, a binomial is not a trinomial and a *Cabralea* is not a *Croton,* nor is a typic variety an atypic one, even as stale bread is not fresh bread, but the names of all these quantities are "Bezeichnungen" in their own right, and it is not what they are in the abstract that counts but *how they react when used.* How do Harms, Mattfeld, and Pilger factually differ from Bolle in regard to handling the trinomial *typicus* or like epithets? So far as it may be gathered, only in their belief that these names are "Bezeichnungen" while Bolle takes them for "Epitheta," a difference which, as it has been shown, rests on the false assumption that a fundamental distinction is established between the two. What is then the *practical* implication of what the three authors write? None that these authors are able to state, beyond uttering the dictum that the proposal to drop *typicus* in the future is useful but not necessary ("ist zwar nützlich, aber nicht erforderlich"). How useful and to what extent neces-

sary, or the other way around, and why, Harms, Mattfeld and Pilger, do not say. The affectation of brevity and pointedness displayed by oracular statements which are not short because they call for controversy, nor pointed because they miss the vitals of an issue, invites Montaigne's comment, as quoted by the elder De Candolle (Théor. Elem. Bot. 310. 1819): "C'est dommage que les gens d'entendement aiment tant la briéveté; sans doute leur réputation en vaut mieux, mais nous en valons moins." (It is a pity that those-in-the-know so like to be brief; no doubt, their fame soars on this account, but we of the common people are left in the lurch.)

In affirming that *typicus* is a "Bezeichnung" in the sense of the Rules ("nach dem Sinne der Regeln") Bolle's opponents appeal to the Rules as if they contain Articles or Recommendations to favor such an appeal. The Rules, in fact, reject it. Article 8 states: "Nomenclature deals with: (1) the *terms* which denote the rank of taxonomic groups (Art. 10–14); (2) the *names* which are applied to the individual groups (Art. 15–72)." In the German text of the Rules the word *terms* is rendered as *Fachausdrücke* (which is clearer, if possible, than its English counterpart), the *names* being known therein as *Namen*. Not a word is said about "Bezeichnungen" of any kind, and Art. 8 leaves no room to quibble, for it specifies the numbers of the Articles which deal with *terms* as against those dealing with *names*. Since the trinomial *typicus* and its equivalents are mentioned for the first time by implication in Art. 18 and Rec. iv, and openly by Rec. xviii following Art. 30, it is patent that this trinomial and its kindred are *names* according to the Rules. They differ, as we have seen, from other names only in one respect; they cannot be transferred unless they are accompanied by the units which they typify. *This is not so much because they have special virtues of their own, and are "Bezeichnungen" rather than "Epitheta," as because certain epithets normally used to connote the type-units below the binomial lend themselves to ambiguity when they are thoughtlessly transferred.* Proof of this statement is in the fact that *Acomastylis elata* var. *genuina* and *A. elata* var. *elata* have the same meaning in taxonomy and the same function in nomenclature; they are absolute synonyms, as a matter of fact, because (see Art. 16) they have the same position (both stand under the same species, *A. elata*) the same circumscription (both are based upon the very same type-specimen), and the same rank (both are varieties). The only difference between these Siamese twins is a matter of detail: *A. elata* var. *elata* can be transferred as easily as any other trinomial—despite its being a "Bezeichnung," not an "Epitheton," if we are to believe certain expounders—while *A. elata* var. *genuina* cannot be transferred without loss of meaning on account of the general nature of the epithets *genuinus* and *typicus*. That a detail, not an essential point is here involved can be further proved by reference to the fact that a taxonomist who intends to publish the

typic variety of *A. elata* is perfectly free to use *genuina* rather than *elata*, or the other way around. He may use either one with the assurance that he will state precisely the same thing, convey the same meaning, be understood in the same sense. That so trifling a difference between *genuina* and *elata*, or any other such set of trinomials, should have engendered lasting confusion, called for a monumental outpour of platitudes, ill-digested notions and loose thought, is truly astounding.

It may be asked whether it is convenient to retain *typicus*, *genuinus* and the like in view of the positive liability which these epithets carry in their bosom when transferred. My opinion is that we must put up with these trinomials because they are already in the record, and it proves impossible to outlaw them without inflicting irreparable damages upon the nomenclature now accepted. Nor is this liability without its compensation, for there is no opportunity for mistaking any trinomial labelled *typicus*, *genuinus*, or the like for a trinomial lacking typic status. As my final thought on the matter, I state my belief that the proper way of dealing with a delicate and exacting piece of machinery is not hitting it with a sledge-hammer, but learning how to use it. A student who intends to prepare himself for botanical work must put up with *typicus* and be ready to master its intricacies, precisely as he must learn to match specimens and to write a tolerable Latin diagnosis, all these being the essential requirements of his craft. Once the proper functions and the correct use of *typicus* are understood and suitable amendments are introduced into the Rules by those who understand these functions and this use, all reasons fall for preferring *typicus* to another trinomial.

As a matter of fact, even under the Rules now in vigor such trinomials as *Acomastylis elata* var. *genuina* must be transferred to *A. Peckii* as *A. Peckii* var. *elata*, not as *A. Peckii* var. *genuina*, for the following reason:

(1) Article 18 states that the nomenclatural type is *permanently* attached to the group which it typifies. True, Art. 18 states at the same breath that the nomenclatural type of a species is a specimen, figure or description. This, however, is belied by the very *Note* in Art. 18 and by Rec. iv and Rec. xviii.

(2) Article 55 orders that the earlier valid epithet must be transferred when a trinomial is moved from one species to the other. This order contradicts the very definition of nomenclatural type given by Art. 18. Accordingly, Art. 18, Art. 55, Rec. iv and Rec. xviii work at cross purposes.

(3) Article 5 states that in the absence of a relevant rule, or when the consequences of rules are doubtful, established custom must be followed.

(4) "Established custom" cannot conflict with Art. 4 which prescribes that forms and names which may cause error and ambiguity or throw science into confusion must be rejected.

In conclusion, since it is patent that *Acomastylis elata* var. *genuina* when transferred to *A. Peckii* as *A. Peckii* var. *genuina* yields a citation which causes error and ambiguity and throws nomenclature into confusion; that the consequences of the Rules are doubtful in the case at hand; that established custom must be followed; that established custom cannot tolerate forms that cause error and ambiguity;—it follows that *A. elata* var. *genuina* must be transferred to *A. Peckii* as *A. Peckii* var. *elata*, because this transfer (a) is factually correct in not altering the typification by specimens in the least; (b) is unequivocal, once the basinym is given and suitable critical notes are furnished. Naturally, no one should forever be expected to reconstruct the Rules where the Rules have broken down, as they have in the present case. Accordingly, the Rules must be suitably modified to take care of the contingencies illustrated in this discussion. However, to sum up, even under the present Rules it is possible to effect the proper transfer of the trinomial *typicus*, as has been shown.

SUMMARY

Two proposals made to amend the existing Rules of International Nomenclature in regard to the typic trinomial (subspecific group *typicus, genuinus*, and the like) are discussed in detail, reaching the conclusion that these proposals are unacceptable. The belief that the trinomial *typicus* differs from other trinomials in essential characters is refuted, and it is shown that the segregation of such a trinomial does not constitute a "new name." In the face of widely circulated misapprehensions the true meaning of Art. 30 and Art. 58 of the current Rules is reestablished. To take care of the inconveniences arising when the trinomial *typicus* is transferred, a modification is proposed to Art. 55, showing at the same time that Art. 18 on the so-called "type method" is shot through with contradictions both in the text and in regard to Rec. iv and Rec. xviii of the current Rules. A brief account is given, based on examples, of the nature and function of the typic trinomial. It is shown how this trinomial can be properly transferred even under the existing imperfect Rules.

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THE STATUS OF CERTAIN ANOMALOUS NATIVE CRAB-APPLES IN EASTERN UNITED STATES

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Well known to anyone who has grown apples from seed is the abandon with which these plants produce viable and fertile hybrid offspring. Intervarietal and interspecific crosses are produced freely, not only among apples but among species of most of the related genera. The several genera of the apple family (or subfamily) have long been noted for this behavior, and much of the distress felt by earnest taxonomic workers in this and other rosaceous groups is traceable directly to it. The combination and recombination of characters brought about by repeated crossing, coupled with the chromosomal irregularities which are often initiated by such hybridization, has made the positive segregation of genetically distinct species almost impossible in certain populations.

In view of this tendency toward hybridization, it is not surprising to find that fertile crosses can be produced between the common cultivated apple on the one hand, and the native American crabapples on the other. There has been little concerted effort to effect experimental crosses of this sort except with stocks of the prairie crab, *Malus ioensis* (Wood) Britton; this one species has been the subject of extensive investigations, chiefly by Professor N. E. Hansen of South Dakota, and some desirable new hardy hybrid stocks and varieties have been produced.[1] Native crabapples are common, however, in eastern United States, especially along the mountain chains from western New York to Alabama and Georgia, and there would appear to have been ample opportunity for cross-fertilization in this region, where the cultivated apple has flourished since its first introduction by the early colonists.

As Professor L. H. Bailey has recently pointed out[2] in connection with his own studies of the blackberries, it is neither safe nor scientifically sound to assume hybridity for puzzling forms which do not fit one's conception of any known species. The principal criteria of hybridity, as he goes on to say, are mostly three in number: "(1) presence of the two [supposed] parents in the vicinity; (2) occurrence usually in small numbers, as if incidental or exceptional to the main population; (3) characters that appear to belong only to the parents in various degrees of combination." Actual proof of hybridity, of course, is sometimes possible by means of self-pollination (or at

[1] See, for example, the following by Professor Hansen: Plant Introductions (1895–1927). So. Dak. Exp. Sta. Bull. 224: 1–64. 1927; ibid. 309: 1–16. 1937; New Hardy Fruits for the Northwest. ibid. 339: 1–31. 1940; Taming the Native American Apple. Rep. So. Dak. Hort. Soc. **36**: 61–62. ?1940.

[2] Gentes Herb. **5**: 7. 1941.

least controlled pollination) of suspected hybrids; hybrid seedlings from continued crosses will eventually reproduce in some measure the combinations of characters found in the original species. Controlled crossing experiments are not always possible, however, especially with woody plants which take several years to come to maturity, so that the student must often content himself with observations on the plants as they occur in nature.

Recently I have had occasion to collect and study material of the native crabapples, and my attention has been focused from time to time upon certain trees which are atypical—trees which appear to be anomalous in the midst of the general population. These peculiar trees, occurring at widely separated localities from Delaware to Georgia and west to Indiana, look at first glance like crabapples which are but a little out of the ordinary. The technical characters are, for the most part, those of the American crabapples, so that any demonstration of their hybrid origin must rest upon their less obvious and perhaps intangible features. The most obvious difference between these nonconformists and the ordinary native crabapple is that in the latter the leaves of vigorous shoots, and sometimes those of the fruit-spurs as well, are provided with broad sharp lobes, so that the blades sometimes simulate those of the red maple. In the aberrant individuals, on the other hand, the blades are less strongly or not at all lobed, and so sometimes resemble those of cultivated apples.

In 1913 Professor Alfred Rehder designated as a new species *Malus platycarpa*, a native crabapple in which the leaves were said to be "oval or elliptic, acute, serrate, not lobed, or sometimes slightly lobed at the end of vigorous shoots." Thus was unwittingly created a convenient repository for any native crabapple with unlobed or slightly lobed leaves; botanists since 1913 have availed themselves of this to such an extent that the name *Malus platycarpa* has lost its specific application and is now used for a whole series of forms which appear to be of hybrid origin. We need not pass here upon the genetic constitution of Rehder's original material, but his description, as will be pointed out below, sounds peculiarly like that of one of our suspected hybrids.

The following table contrasts briefly the more obvious features of the cultivated apple with equivalent ones pertaining to the American crabapples of the Section *Chloromeles* (Decne.) Rehder;[3] the latter are considered as a

[3] It should be noted that if the name Sect. *Chloromeles* be used for the group of the American crabapples, it then becomes necessary to revive Sect. *Calycomeles* Koehne (Deutsch. Dendr. 257. 1893) for the group called by Rehder Sect. *Eumalus* Zabel. Koehne's Section *Calycomeles* originally comprised all the species of *Malus* supposed by him to have a persistent calyx, including the American species *M. coronaria* and *M. angustifolia*, five Old World species having involute unlobed leaves (now referred by Rehder to *Eumalus*), and *M. "crataegifolia"* (*M. florentina* (Zuccag.) Schneid.), now referred by Rehder to a subsection of Sect. *Sorbomalus*. This latter species was apparently included in *Calycomeles* by an oversight or error, since according to Schneider and Rehder it has a deciduous calyx.

unit, the several species agreeing closely in technical characters. Also contrasted below are the characters of the series of plants called *Malus platycarpa*, including not only the original *platycarpa* of Rehder, but also certain other native plants, referred to above, which have various features in common.

A Cultivated Apple	B "*Malus platycarpa*"	C Other American Crabs of Section *Chloromeles*
Trunk becoming thick in age, often more than 30 cm. in diameter.	Trunk reaching a maximum diameter of at least 35 cm.	Trunk usually 15 cm. in diameter or less, sometimes reaching 25 cm.
Branches not thorny.	Branches thorny or in some plants not at all so.	Branches usually definitely thorny.
Leaves rolled (involute) in the bud.	Leaves folded (conduplicate) in the bud	
Leaves never lobed normally, even on vigorous shoots.	Leaves usually unlobed, or those of vigorous shoots lobed.	Leaves regularly lobed, or those of the fruit-spurs unlobed.
Fruits various in size, often 5–10 cm. in diameter.	Fruit often 4–6 cm. in diameter.	Fruit usually not more than 4 cm. in diameter.
Fruit usually red or yellow, or red-cheeked.	Fruit green, yellow, or red-cheeked.	Fruit green, yellowish-green or yellow.
Fruit with a small depression at apex, the core united with the flesh and its apex not protruding.	Core with a free pointed apex not fused with the flesh of the fruit.	
Pedicels short and stout, usually 1–2.5 cm. long, and up to 2 mm. in diameter.	Pedicels nearly like those of group C, but sometimes shorter and stouter.	Pedicels slender, often 3–4 cm. long, about 1 mm. in diameter (exceptions in Ohio–Indiana region and w.)
Pedicels and outer surface of hypanthium densely pubescent at flowering time.	Pedicels and hypanthium usually pubescent, sometimes densely so.	Pedicels and outer surface of hypanthium glabrous (exceptions as above and pedicels sometimes sparsely pilose).
Anthers pale yellow.	Anthers pink or salmon color, or yellow with almost no pink.	Anthers pink or salmon-color.
Flowering season early.	Flowering season that of group A or slightly later.	Flowering season late.

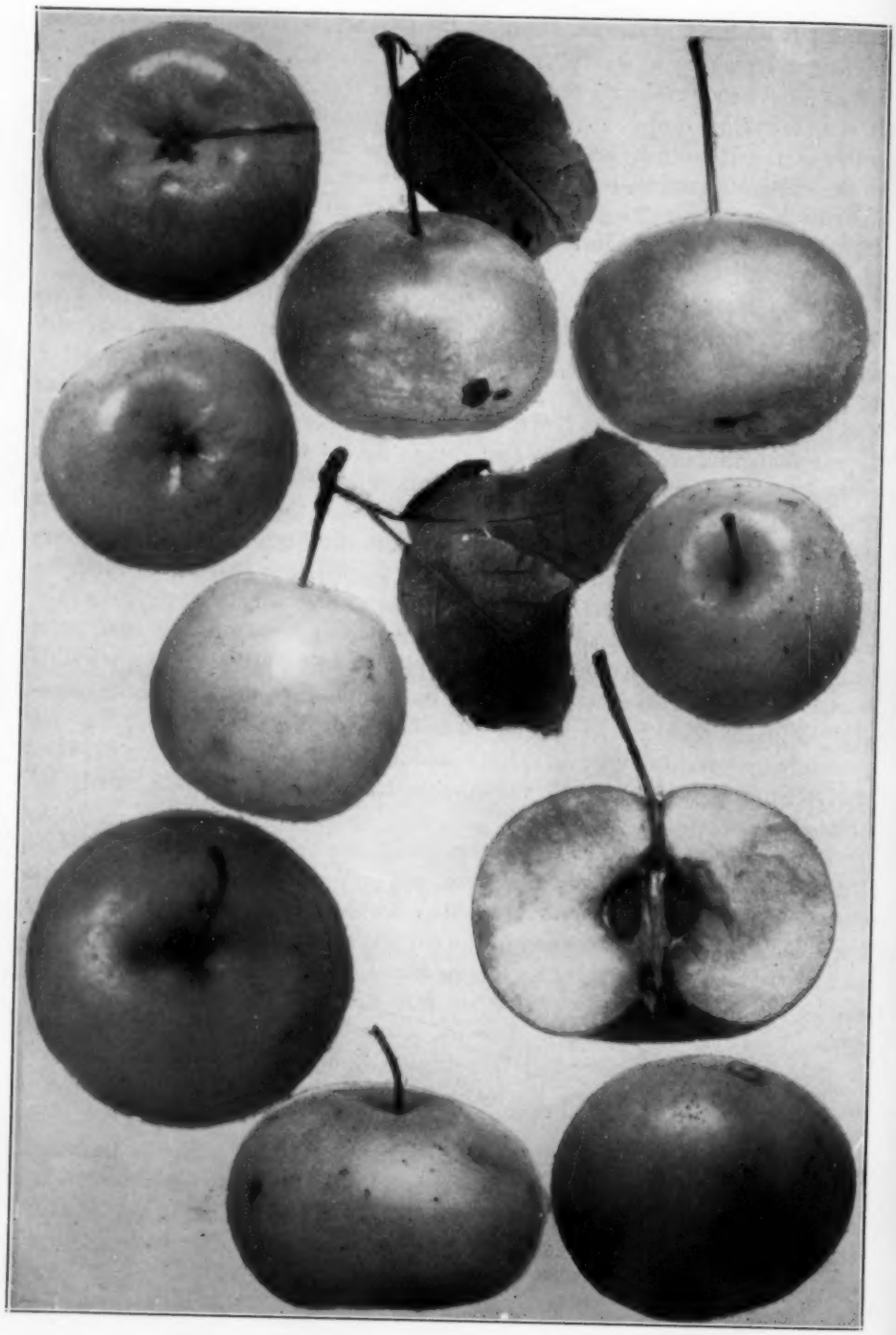
It is at once evident, upon inspection of the table, that the "*platycarpa*" group is morphologically intermediate between the American crabs and the cultivated varieties, showing an undoubted affinity to the former. Professor Bailey's third criterion of hybridity, the appearance in the supposed hybrid of characters belonging to the two parents, may be abundantly tested with

The section *Calycomeles* may accordingly be typified by one of the remaining species. Since Rehder has already typified his section *Chloromeles*, basing it upon *Malus angustifolia* (Jour. Arnold Arb. 2: 49. 1920), there is left in *Calycomeles* a group of species all of which have been included by recent authors in *Eumalus*. Since *Calycomeles* (1893) antedates *Eumalus* (1906) it is necessary to employ the former when using it as the name of a section. The Section *Calycomeles* may be typified by *Malus sylvestris* Mill.

respect to *Malus platycarpa*. Many of the characters of the American crabs appear to be wholly or partially dominant, so that all the supposed hybrids which I have seen resemble these species rather markedly. In this connection it is noteworthy that crabapples of known hybrid ancestry, specifically a series of the Hansen hybrids between forms of *Malus ioensis* and varieties of the cultivated apple, resemble the former very strongly. A series of these hybrids is available for study at the U. S. Plant Introduction Garden at Glenn Dale, Maryland; in all characters of leaves and branchlets they are strikingly similar to the *ioensis* parent.

Although trees of the supposed "*platycarpa*" stock have certain features in common, the stock is by no means a homogeneous one. Trees from different localities differ markedly in characters of the branches (chiefly in the greater or lesser number of thornlike branchlets present), in leaf-shape, and in size and other characters of the fruit. The fruits of "*platycarpa*," while usually larger than those of the native crabapples, are as variable as might be expected among the offspring of the hundreds of varieties of cultivated apples. They vary in shape from flat or depressed-globose (the shape of the original *platycarpa*) to globose (sometimes even becoming higher than broad); one tree near Andrews, North Carolina, bears apples of a sheep-nose type. In color these fruits vary from a dull green like that of some native crabs to a clear pale yellow not unlike that of the Transparent, or to a red-cheeked form resembling some of the cultivated crabapples. It seems altogether improbable that fruits of such diverse types should be produced by a single species, especially since no other native species is known to vary in this way, and it seems probable that the different sorts have arisen following hybridization between native apples and cultivated varieties which are distinguished chiefly by fruit-characters (figs. 1, 2).

In almost all the other characters which are readily studied, plants of *Malus* "*platycarpa*" resemble the American apples rather than the European one; it is even possible, moreover, to suggest which of several species of native crabs may have been concerned in the supposed cross, chiefly through study of leaf-characters. In the region where *Malus angustifolia* is the only native apple, the southeastern Coastal Plain and Piedmont, the leaves of "*platycarpa*" invariably approach those of *angustifolia* in shape and petiole-length; between Baltimore and Wilmington, however, where several colonies of "*platycarpa*" are known, the leaf-shape and petiole-length of these plants approach that of *M. coronaria*, the prevailing species of that region (see figure 3). In areas like that in the vicinity of Asheville, North Carolina, where both *M. angustifolia* and *M. coronaria* and its relatives occur, it has not been possible to distinguish between the effects of the two species in crosses with cultivated varieties.



A character which is doubtless related to the genetic constitution of any given plant, but which is not readily evaluated except by comparative and simultaneous studies on whole series of plants, is that of date of flowering. This date is influenced to a considerable extent by regional and local climates and by other factors, and so varies somewhat from place to place and from year to year. Different species and varieties of apples, however, appear to bear a reasonably constant relation to each other in this respect. Where *Malus glabrata*, *M. coronaria*, and *M. angustifolia* grow together, the flowering period of the first two is a week or ten days ahead of that of *M. angustifolia*, and is slightly preceded in its turn by the flowering of the cultivated apples. This relation appears to obtain regardless of season or locality. One would expect, therefore, that hybrids of *Malus angustifolia* would be met with infrequently, because of the rather considerable discrepancy between its flowering period and that of the cultivated stock. This is borne out in practice, so far as I have observed; most of the plants of "*platycarpa*" have been found in areas where *M. coronaria* is the only native species known to occur. *Malus glabrata* is not taken into consideration, as it is a rare species confined to high coves in the mountains of western North Carolina.

Plants of *Malus "platycarpa"* regularly flower with or slightly later than cultivated apples in the same vicinity, and considerably ahead of plants of *M. angustifolia*, but precede *M. coronaria* not more than a few days. In the vicinity of Washington, D. C., on April 19, 1942, thickets of "*platycarpa*" apples were budding, with pink-balloon-like petals just beginning to separate; in the same fields, immediately adjacent to these trees, were cultivated apples in full bloom, while in Rock Creek Park not more than two miles away the native *M. angustifolia* had not yet begun to show pink in its tiny buds. Near Newark, Delaware, and near Baltimore, Maryland, on May 3, 1942, orchards had passed the height of their bloom and plants of *Malus "platycarpa"* were dropping their petals, while nearby plants of *M. coronaria* were still partially in bud. At the foot of Lookout Mountain, in Dade County, Georgia, on April 27, 1941, a "*platycarpa*" tree had dropped most of its petals, as had cultivated trees; native trees in identical situation a few miles down the valley were just coming into flower. Two days later, near Blue Ridge, in Fannin County, Georgia, a specimen of *Malus "platycarpa"* was in full bloom along the road, in marked contrast to nearby specimens of *M. angustifolia* that were yet in bud.

Explanation of figure 1.

Fruits of supposed hybrid crabapples, natural size. Three large fruits in upper row are from *McVaugh 5441*, Virginia, neg. 77765; three small round fruits in center are from *McVaugh 5462*, Maryland, neg. 77789; bottom row and the cut fruit are from *McVaugh 5497*, Virginia, neg. 77917. Note variation in size, shape, color values, degree of glaucosity, and length of stem. Negative numbers refer to photographs in the files of the Division of Plant Exploration and Introduction.

In regard to the second of the criteria of hybridity mentioned above, namely the presence of the two supposed parents in the vicinity of the suspected hybrid, it is noteworthy that most if not all the known occurrences of *Malus "platycarpa"* have been in or near inhabited places where both

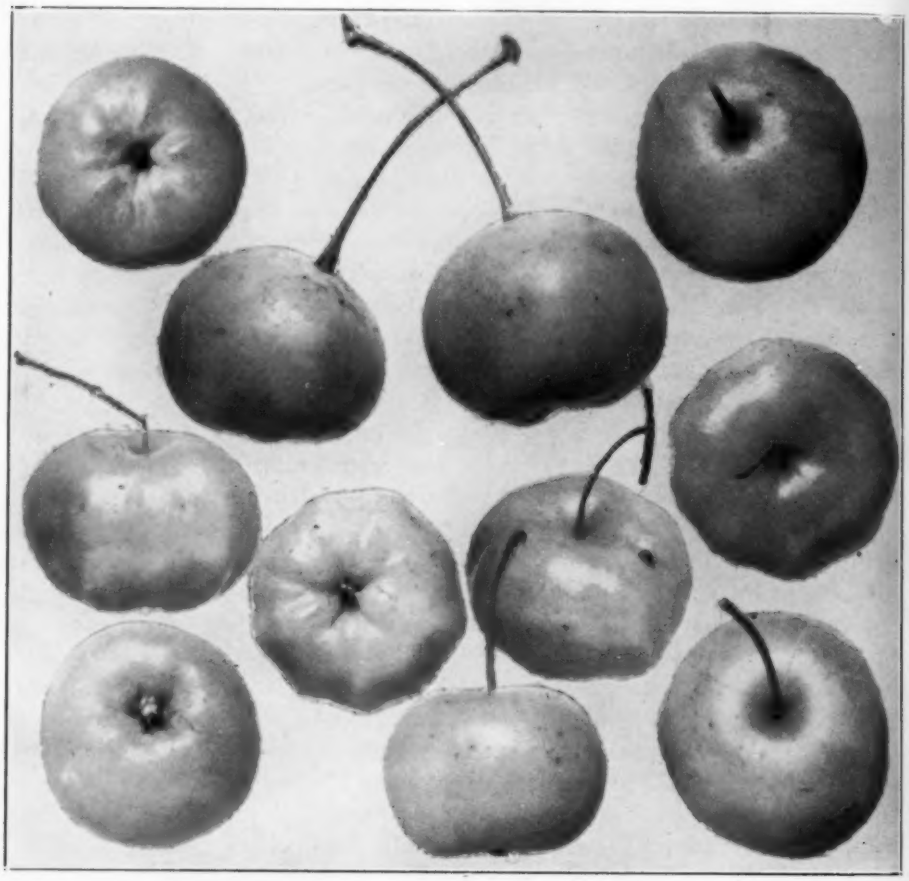


FIG. 2. Fruits of native American crabapples, natural size. Top row, *Malus angustifolia* (Ait.) Michx., from a collection by O. M. Freeman, District of Columbia. The fruit is often lopsided (second from left) and the thickened peduncle is characteristic. Neg. 77763. Second row, *Malus glabrata* Rehd., from *McVaugh 5495*, a cultivated tree at Ithaca, New York. The fruit is yellow and characteristically flattened and angled; Neg. 77906. Bottom row, *Malus coronaria* (L.) Mill., from *McVaugh 5443*, Perry Co., Pennsylvania; Neg. 77764.

native and cultivated apples were also known. *Malus platycarpa* var. *Hoopesii* (Rehd.) Rehd., one of the many forms of *"platycarpa"* as that group is understood in this paper, originated in a nursery at West Chester,

Pennsylvania, and was sent to the Arnold Arboretum in 1876. According to notes made by T. G. Harbison, who collected the original specimens of *Malus platycarpa,* the species occurred as "scattered trees . . . near Franklin [North Carolina] at a distance of from 3 to 15 miles from the [original] locality." Harbison is also quoted as saying "As this tree grows in the fertile soil of bottoms it has been nearly exterminated by the clearing of the valleys."

In 1929, Doctor S. F. Blake discovered a thicket of "*platycarpa*" crabapples in Arlington, Virginia, on the outskirts of Washington, and more recently additional trees have been found a few miles further south, near the Arlington-Alexandria boundary. A thicket comprising thousands of plants of vigorously growing crabapples borders the main highway to Philadelphia at the eastern boundary of the City of Baltimore, where these trees seem to compete favorably with ordinary wild plants in the vicinity. Further northeast, just south of Newark, Delaware, in a long-settled and intensively farmed area, several large trees of "*platycarpa*" occur in a pasture. Further south and west suspected hybrids occur along roadsides near McArthur, Ohio, near Hendersonville, North Carolina, and at several places in northern Georgia.

It is not always possible, naturally, to find cultivated apples, native crabs, and the putative hybrids between them, all growing happily together in the same thicket. In all the localities enumerated above, however, both possible parent types are known to occur, either in the immediate vicinity of the supposed hybrids, or, at most, at distances of a few miles. Cross-pollination by insects is often effected over distances of this order of magnitude, and birds, or other animals, frequently carry seeds or whole fruits to similar distances from the parent plants, so that in this one respect a hybrid origin for all the known plants of *Malus "platycarpa"* is entirely possible.

The third criterion of hybridity, again to quote Professor Bailey, is "occurrence usually in small numbers, as if incidental or exceptional to the main population." Without exception the plants of *Malus "platycarpa"* known to me are isolated or anomalous trees, local in occurrence and differing markedly from the remainder of the apple population in the vicinity. There are apparent exceptions to this near Baltimore and near Washington where *Malus "platycarpa"* reproduces exceptionally well by seed, forming extensive thickets. A clue to this behavior is found, however, in the fact that the seedlings making up these thickets agree with their elders exactly, leaf for leaf and feature for feature. Other species of *Malus,* and species of related genera, including *Crataegus,* are known to behave in exactly this fashion; triploid and other types, apparently of hybrid origin, come true from seed even when exposed to foreign pollen. Some of these do not develop viable pollen of their own and are thought to have developed an apogamous or par-

thenogenetic process by which fertile seeds are produced in the absence of any fertilization whatever. Few of the "*platycarpa*" plants have been investigated cytologically,[4] but such an investigation is highly desirable and might settle finally the question of the hybrid origin of these forms. Chromosome counts have been made upon some of the hybrids developed by Professor N. E. Hansen in South Dakota. One of these, Kola, was determined to be a tetraploid ($2n = 68$) by Nebel;[5] other varieties have been investigated by Professor F. B. Lincoln of the University of Maryland, who finds that the chromosome number varies from 34 in some varieties to 51 or 68 in others. The parents of the triploid and tetraploid varieties are themselves said to be normally diploid.[6]

The total of the evidence at hand, although this evidence is chiefly inferential, indicates a probable hybrid origin for a series of forms which have been known collectively as "*Malus platycarpa.*" Although it is clearly unsafe to predicate the hybrid nature of plants known from herbarium specimens alone, it appears from such specimens and from the description of *Malus platycarpa* var. *Hoopesii* and the original *M. platycarpa* of Rehder that these are also to be regarded with suspicion.

Some of the collections referred by botanists to *Malus platycarpa* may have been taken from aberrant individuals of genetically pure species, but it is highly improbable that the entire series of plants discussed in this paper has arisen through variation alone. Much additional information is needed in order satisfactorily to establish the status of these anomalous trees, and botanists and collectors will do well to make ample notes and full collections from them at every opportunity.

Following is a discussion of the material upon which the present paper is based:

DELAWARE: Three miles south of Newark, Newcastle Co., *McVaugh 6494.*[7] Several round-headed open-grown trees in a pasture, the largest about 8 m. tall and with a single trunk about 35 cm. dbh. Branches not at all thorny; leaves slightly lobed on vigorous shoots; pedicels definitely hairy; petals almost all fallen on May 3, 1942; fruit somewhat flattened, not over 4 cm. in diameter, resembling that of native species. Native species are not abundant in this vicinity, but are known to occur locally near Christiana (about 10 miles away) and in southeastern Chester Co., Pennsylvania (at about the same distance).

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[4] A report of the occurrence of tetraploidy ($2n = 68$) in *Malus platycarpa* was made recently by F. B. Lincoln and L. P. McCann (Proc. Am. Soc. Hort. Sci. **34**: 26. 1937), but the source of the material was not stated and there appears to be no way to check its authenticity.

[5] Gartenbauwiss. **1**: 549–592. 1929.

[6] Proc. Am. Soc. Hort. Sci. **37**: 217. 1940; S. Dak. Exp. Sta. Bull. 339: 11. 1940.

[7] Herbarium specimens cited in this paper, unless otherwise indicated, are deposited in the Herbarium of the United States National Arboretum, Washington, D. C.

MARYLAND: Along U. S. Highway No. 40, east of Baltimore City Limits in Baltimore Co., *McVaugh 5462* (Sept. 29, 1940, in fruit) and *5500* (April 20, 1941, in bud). Hundreds of vigorous plants forming extensive thickets over an area more than a mile long; the plants commonly have an upright habit quite distinct from that of the ordinary native apple. Branches not at all thorny; leaves slightly lobed on vigorous shoots; pedicels white-tomentose; petals fallen and fruit slightly enlarged on May 3, 1942; Fruit 3.1–3.7 cm. in diameter, 2.8–3.4 cm. high, greenish-yellow, glaucous, faintly odorous and very slightly waxy; seeds none, or 1–4. Native species are not abundant in this region, but plants occur locally at points 1–5 miles distant. Figures 1, 3.

VIRGINIA: 1. Thickets at corner of Glebe Road and Washington Boulevard, Arlington, *McVaugh 5497* (October 24, 1940, in fruit). From the same thicket, *S. F. Blake 10831* (April 23, 1929, in flower, Oct. 15, 1929, in fruit). About twenty scattered plants on gravelly overgrown hillsides. Branches somewhat thorny; leaves slightly lobed on vigorous shoots; buds beginning to open on April 19, 1942; fruit flattened, 3.9–5.2 cm. in diameter, 2.9–3.5 cm. high, yellowish-green, glaucous, fragrant and slightly waxy; seeds usually about 5. Native crabapples are scarce in this region; a few supposedly native plants of *Malus angustifolia* are known from the District of Columbia. Figures 1, 3.

2. Abandoned pasture, lowlands called "Hell's Bottom," south of Columbia Pike and east of Arlington Ridge Road, Arlington, *McVaugh 5441, 5442* (September 15, 1940, in fruit). Specimens from the same locality, *F. R. Fosberg 16971* (flower) and *17432* (fruit), are to be distributed. About twenty small trees associated with cultivated apple (seedlings?). Branches not or but slightly thorny; leaves lobed on shoots, suggesting the shoot-leaves of *Malus angustifolia* (fig. 3); pedicels hairy; buds "ballooned" on April 19, 1942; fruit flattened, 3.5–4.5 cm. in diameter, 2.5–3.5 cm. high, greenish-yellow, usually with a red cheek, glaucous, almost without fragrance and waxy covering (fig. 1); seeds 4–10.

NORTH CAROLINA: 1. Roadside thickets 4.5 miles north of Hendersonville, Henderson Co., *McVaugh 5632*. A single tree about 6 m. tall, with spiny branches, associated with *Malus angustifolia* and cultivated apples. Leaves not lobed; plant in full bloom on April 30, 1941, when *M. angustifolia* in the same thicket was still partially in bud; pedicels hairy or tomentose; anthers yellow or very faintly pinkish; fruit unknown. Native crabapples are abundant in this region.

2. Roadside 3.4 miles west of Franklin, Macon County, *McVaugh 5624*. A single plant; branches not spiny; growth and bark like those of the cultivated apple; leaves very slightly lobed on vigorous shoots; plant in full bloom on April 29, 1941, slightly in advance of nearby trees of *M. angustifolia;* pedicels hairy; anthers cream-yellow, slightly pink-tinged; fruit unknown. Native crabapples are abundant in this region.

3. Edge of cultivated field 4.2 miles northwest of Andrews, Cherokee Co., *McVaugh 5618*. A single open-grown tree about 6 m. tall, the branches scarcely spiny; leaves somewhat lobed on vigorous shoots; pedicels hairy; flowers almost all open on April 29, 1941, somewhat in advance of nearby native trees; fruit of the last (1940) season fallen at this date, mostly about 4 cm. in diameter, a little longer than broad, slightly sheep-nosed. Native apples are not abundant in this region, but occur sparingly throughout.

FIG. 3. Leaves of representative American crabapples and supposed hybrids, in seven groups. Each group comprises two or more leaves from a single tree, including the following types; 1) A large leaf from a vigorous shoot; this leaf indicates the maximum size and maximum degree of lobing for the tree in question. 2) Leaves from the base of vigorous shoots or those produced by fruit-spurs after the flowering season; these two types are indistinguishable. Leaves of this sort are regularly smaller and narrower than the lobed leaves from vigorous shoots. 3) Small leaves from the fruit-spurs; these are present at flowering time and persist until late in the season; they are usually not lobed except in *M. glabrata* and in forms of *M. coronaria* and *M. ioensis*. Neg. 79705. All leaves about $\frac{2}{3}$ natural size.

Bottom row, left to right:

M. "platycarpa," McVaugh 5462, Baltimore, Maryland. Note the relatively long petioles in this group and two following.

M. coronaria (L.) Mill., *B. Long 16985* (in herb. Morris Arboretum), from Newcastle Co., Delaware (three largest leaves), and *McVaugh 6495*, Chester Co., Pennsylvania (two small leaves). Note that lobed and unlobed leaves may be found on the same plant. Some forms of *M. coronaria* have more strongly lobed leaves, with sharper serrations, than do those shown here.

M. "platycarpa," McVaugh 5765, Vinton Co., Ohio.

Top row, left to right:

M. angustifolia, McVaugh 5227, Talbot Co., Georgia. This is not an unusual leaf-form in this species, although forms with crenate leaves are common. Note the short petioles in this group and the three following.

M. platycarpa Rehd., *Harbison*, "April 22, 1911," from Macon Co., North Carolina (in U. S. National Herbarium). The date is apparently erroneously given; the maturity of the specimen indicates that it was collected in the fall.

M. "platycarpa," McVaugh 5497 (two at top) and *Blake 10831* (at bottom), Arlington, Virginia.

M. "platycarpa," McVaugh 5441, Arlington, Virginia.

GEORGIA: 1. Roadside, edge of field, 2.2 miles east of Blue Ridge Hotel, Blue Ridge, Fannin Co., *McVaugh 5614*. A single open-grown tree about 6 m. tall; branches not spiny; growth and bark like those of the cultivated apple; leaves not lobed; pedicels and calyx hairy; plant in full bloom on April 29, 1941, slightly in advance of trees of *M. angustifolia* in the same valley about 2 miles further west; fruit unknown.

2. Pasture on Bible Farm 1 mile north of Sulphur Spring Station, Dade Co., *McVaugh 5594*. A single open-grown tree about 8 m. high. Branches not spiny; leaves not lobed; pedicels and calyx more or less tomentose; petals almost all fallen on April 27, 1941; on the same day *Malus angustifolia* at Valley Head, Alabama (also at the foot of Lookout Mountain) was in full bloom, and at the summit of Lookout Mountain near DeSoto Falls the same species was in bud. Native crabapples are abundant in this region.

OHIO: Roadside bank in woods above stream, 4 miles northwest of McArthur, Vinton Co., *McVaugh 5765*, July 4, 1941. A single tree about 5 m. tall; branches scarcely spiny; leaves and habit like those of the cultivated apple, the leaves not at all lobed except on the most vigorous shoots; pedicels hairy at the above date; flowers and mature fruit unknown; core of immature fruit that of the section Chloromeles. Figure 3. Native crabapples occur throughout this region.

SUMMARY

At various localities in eastern United States occur trees which are certainly derived from native American sources but which do not comprise a homogeneous stock and which 1) Occur as anomalous or isolated individuals or groups in the midst of undoubted native populations, and 2) are morphologically and physiologically intermediate between native species and the introduced, cultivated apple. This series of forms is usually characterized by fruit larger than that of the American crabapples and by leaves possessing a lesser degree of lobing than those of the native species. Most of these forms have been called "*Malus platycarpa* Rehd." or "*Malus platycarpa* var. *Hoopesii* (Rehd.) Rehd." It is inferred from observation and from comparison with hybrids of known parentage that most, if not all, of the plants previously referred to *Malus platycarpa*, including probably the original material and that of var. *Hoopesii*, are of hybrid origin. It is supposed that hybridization has taken place between cultivated apples and native species of *Malus*, section *Chloromeles*, occurring in the same region. Experimental proof is needed to confirm this hypothesis.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION,
BUREAU OF PLANT INDUSTRY,
U. S. DEPARTMENT OF AGRICULTURE, BELTSVILLE, MD.

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CHROMOSOMES OF ASTRAGALUS

HILDA VILKOMERSON

Some species of *Astragalus* absorb and accumulate selenium from seleniferous soils; other, closely related species do not (15). Preliminary to a genetic study of this physiological variation, a survey was made of the chromosome number relationships in 26 North American species of *Astragalus*, whose responses to selenium have been determined by Beath and by Trelease (1, 15).

Germinating seeds of the various species were obtained from Prof. Sam F. Trelease. Chromosome numbers were counted from metaphase plates of seedling root-tips fixed in Craf (modified Navashin) fluid, sectioned at 12 μ (Randolph's card technique (8) being used for handling large numbers of roots), and stained with Newton's crystal violet–iodine.

Of the 26 species studied, 11 have 24 chromosomes (2n; fig. 1). All these are selenium absorbers, as is also the one 44-chromosome species (fig. 2). One species, a non-absorber, has 16 chromosomes (fig. 3). Thirteen species have 22 chromosomes (fig. 4), and of these, four are selenium absorbers, nine non-absorbers.[1] From Table 1 it is evident that members of the *Lonchocarpi* or of the *Podo-sclerocarpi* groups are the desirable species for genetic study of selenium absorption, since these groups include species of like chromosome number and unlike reaction to selenium.

With a single exception, the karyological evidence supports the taxonomic grouping of M. E. Jones' revision of the genus (4). His group *Galegiformes*, however, includes species which differ both in selenium response and in chromosome number (*Astragalus Drummondii* and *A. racemosus*). According to Rydberg's classification (12), too, these species would be grouped together in the genus *Tium* (table 2). Likewise, the cytological findings do not support the unity of Rydberg's genus *Cnemidophacos*. Physiologically this group of species is homogeneous; but here the disparity in chromosome number is paralleled by considerable morphological divergence (4). Indeed, Rydberg in earlier treatments of this material (9, 10) had recognized this difference by using two generic names—*Cnemidophacos* for *A. flavus* and *A. confertiflorus*, and *Ctenophyllum* for *A. Grayi* and *A. pectinatus*. Gray made a like distinction (3). As for Rydberg's *Phaca Preussii*, his earlier grouping of

[1] One species of the very closely related genus *Oxytropis*—*O. pinetorum* (Heller) Rydb. (*O. saximontana* Nels.), which is an important "loco" weed, though not a selenium absorber—was studied. The 2n number is 48. Some so-called loco weeds actually belong in the genus *Astragalus* (e.g., *A. mollissimus* and *A. Earlei*); seedlings of these, however, were not available for study.

this species with *Jonesiella Pattersoni* and *J. praelongus* (11) would seem justified.

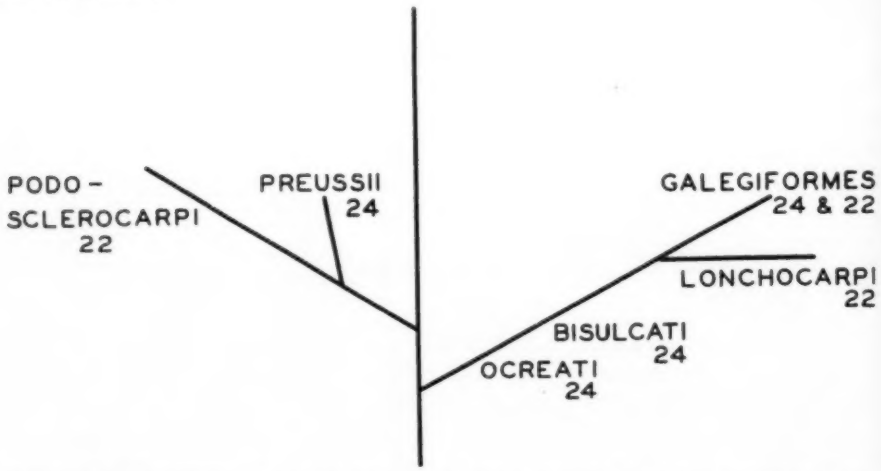
In previous cytological studies of *Astragalus*, ten workers (14) have reported chromosome numbers for 44 Old World species and 4 New World

TABLE 1

Species (Jones' revision)	Selenium absorption	Chromosome number (2n)
Inflati		
Astragalus lentiginosus var. *palans* Jones	–	22
Podo-sclerocarpi		
A. toanus Jones	+	22
A. rafaelensis Jones	+	22
A. Grayi Parry	+	44
A. pectinatus Dougl.	+	22
A. Casei Gray	–	22
A. pterocarpus Wats.	–	22
A. tetrapterus Gray	–	22
A. sclerocarpus Gray	–	22
A. cañonis Jones	–	22
Preussii		
A. Preussii Gray	+	24
A. limatus Sheld.	+	24
A. Pattersonii Gray	+	24
A. praelongus Sheld. (*Pattersonii* var.)	+	24
A. Beathii Porter	+	24
Uliginosi		
A. canadensis Tourn. in L. (= *A. carolinianus* MacMill., not L.)	–	16
Sarcocarpi		
A. crassicarpus Nutt.	–	22
Ocreati		
A. confertiflorus Gray	+	24
A. flavus Nutt. (*confertiflorus* var. *flaviflorus* Kuntze)	+	24
Bisulcati		
A. haydenianus Gray	+	24
A. bisulcatus (Hook.) Gray	+	24
A. oocalycis Jones	+	24
Galegiformes		
A. racemosus Pursh	+	24
A. Drummondii Hook	–	22
Lonchocarpi		
A. Osterhoutii Jones	+	22
A. lonchocarpus Torr.	–	22

species. Thirty-three of these have the 2n number 16, three species have 32, one 36, four 48, five 64, and one 96. There is one 28-chromosome species. Both Senn (13) and Kreuter (6, 7) emphasize the consistency of the basic chromosome number 8 throughout the Galegeae, and the latter cites *Astragalus* as an "especially beautiful example" of this uniformity. Even though

only a small percentage of the species of this enormous genus has been studied (it contains some 1500 species), this strict uniformity is not wholly borne out by the data on our North American species. To fit the pattern of the species previously studied (basic numbers 7 and 8), we might derive the 24- and 22-chromosome groups from hybrids of species with 32 and 16 chromosomes and 28 and 16 chromosomes, respectively. Such triploid species would be highly unstable, however, owing to irregular meiotic pairing. The 22-chromosome group could have arisen by aneuploid loss from a 24-chromosome form. Indeed Kreuter (7) indicated the possibility that further study might be expected to show *Astragalus* species which had "arisen by a diminution" of chromosome number. Somewhat suggestive of such a relationship is this portion of the phylogenetic tree proposed for *Astragalus* in Jones' monograph. (The selenium-absorbing species, apparently, are restricted to these two branches.)



But in the Leguminosae, as in the Cruciferae, aneuploidy is a common relation between tribes and between genera, but not within genera (13). There remains, then, only the assumption of the basic numbers 8, 11, and 12 for our species.

The sporadic occurrence of isolated polysomatic cells is not uncommon in *Astragalus*, nor is it restricted to this genus of the Leguminosae. Tschechow

TABLE 2

Species (Rydberg's revision)	Selenium absorption	Chromosome number (2n)
Homalobus podocarpus (Hook.) Rydb. (*A. sclerocarpus*)	–	22
Diholcos bisulcatus (Hook.) Rydb.	+	24
D. haydenianus (Gray) Rydb.	+	24
D. oocalycis (Jones) Rydb.	+	24

TABLE 2 (*Continued*)

Species (Rydberg's revision)	Selenium absorption	Chromosome number (2n)
Cnemidophacos flavus (Nutt.) Rydb.	+	24
C. confertiflorus (Gray) Rydb.	+	24
C. toanus (Jones) Rydb.	+	22
C. rafaelensis (Jones) Rydb.	+	22
C. Grayi (Parry) Rydb.	+	44
C. pectinatus (Dougl.) Rydb.	+	22
Xylophacos Casei (Gray) Rydb.	–	22
Pterophacos pterocarpus (Wats.) Rydb.	–	22
P. tetrapterus (Gray) Rydb.	–	22
Lonchophaca macrocarpa (Gray) Rydb. (*A. lonchocarpus*)	–	22
L. Osterhoutii (Jones) Rydb.	+	22
Phaca Preussii (Gray) Rydb.	+	24
P. Crotalariae Benth. (*A. limatus*)	+	24
Tium Drummondii (Dougl.) Rydb.	–	22
T. racemosum (Pursh) Rydb.	+	24
T. palans (Jones) Rydb.	–	22
Brachyphragma Serenoi (Kuntze) Rydb. (*A. cañonis*)	–	22
Jonesiella Pattersoni (Gray) Rydb.	+	24
J. praelonga (Sheld.) Rydb.	+	24
Astragalus canadensis L.	–	16
Geoprumnon crassicarpum (Nutt.) Rydb.	–	22

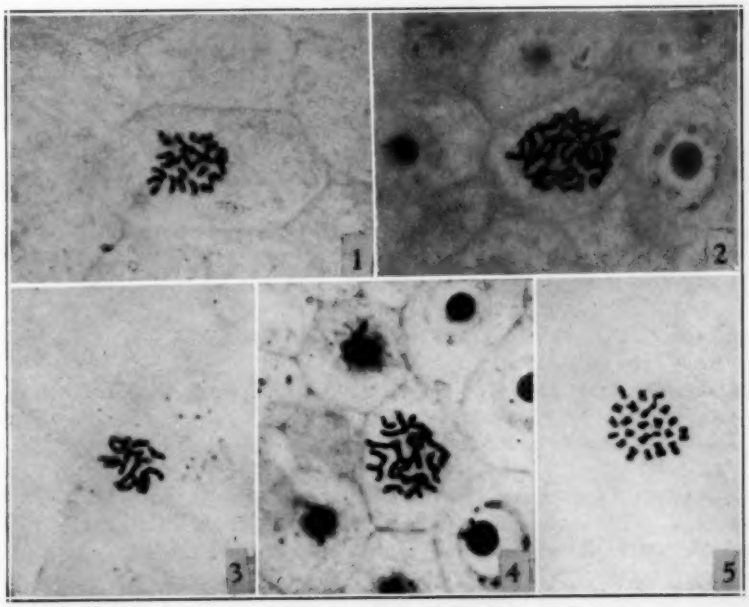


FIG. 1. Somatic metaphase of *Astragalus Preussii* (2n = 24). FIG. 2. *A. Grayi* (2n = 44). FIG. 3. *A. canadensis* (*carolinianus*) (2n = 16). FIG. 4. *A. toanus* (2n = 22). FIG. 5. Polysomaty in *A. cañonis*, showing 22 pairs of chromosomes. In later divisions, such cells show 44 chromosomes, unpaired.

(16, 17) reported such cells in two of the species he studied—*A. altaicus* and *A. candidissimus*. In the latter, indeed, he sometimes found tetraploid numbers (syndiploid he calls them) in up to 40 per cent of the metaphase plates. In our material such cells were found in three of the species studied—*A. Drummondii*, *A. toanus*, and *A. cañonis*—but here they were very rare (fig. 5). Polysomatic cells have been reported, in varying degrees of frequency, for species of several other leguminous genera: *Acacia*, *Albizzia*, *Canavalia*, *Cassia*, *Cicer*, *Glycine*, and *Phaseolus* (2, 5, 6, 17).

SUMMARY

Chromosome numbers are reported for 26 North American species of *Astragalus* and are correlated with selenium absorption data. Possible phylogenetic interrelations are discussed. Polysomaty is reported in three species.

The author is grateful to Professors M. M. Rhoades and Sam F. Trelease for their interest and helpful suggestions.

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BULLETIN OF THE TORREY BOTANICAL CLUB
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INJURIES TO TREES CAUSED BY CELASTRUS AND VITIS[1]

H. J. LUTZ

Observations by the writer over a period of years have revealed that bittersweet (*Celastrus scandens* L.) and grape (*Vitis aestivalis* Michx., *V. vulpina* L., *V. labrusca* L., and *V. bicolor* Le Conte) vines cause distinctive injuries to the stems and branches of young trees. These climbers, which are common or locally abundant in the forests of the eastern United States, are relatively intolerant of shade and are encountered most frequently in stands of young trees, in understocked stands and near forest borders. In other words, they are most abundant in stands representing early stages of suc-

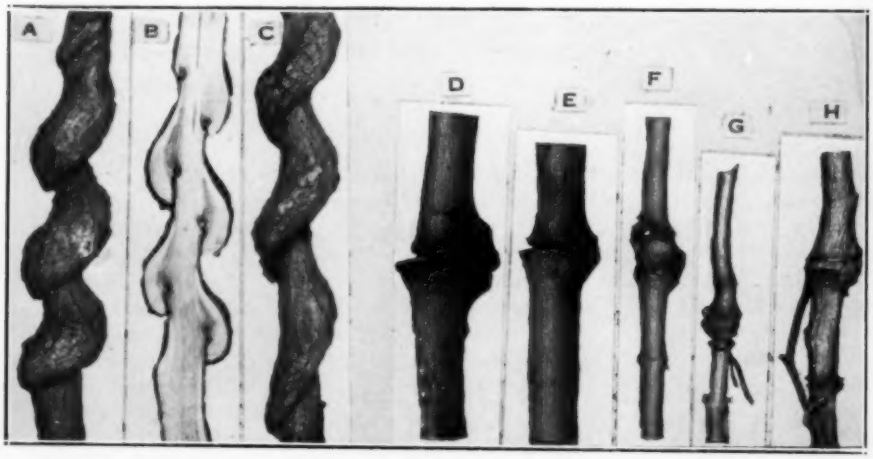

FIG. 1. A, B, and C, stems of *Sassafras albidum* (Nutt.) Nees. showing the injury caused by *Celastrus scandens* L. B, a longitudinal section through the stem A (1/10 natural size). D to H, stems injured by *Vitis* spp. D, E, and F, *Acer rubrum* L. G, *Acer saccharum* Marsh. H, *Hamamelis virginiana* L. (¼ natural size).

cessional development; as stand density increases the number and vigor of the vines decreases. South and west slopes appear more favorable for their development than are north and east slopes. Other vines such as poison ivy (*Rhus toxicodendron* L.) and the Virginia creeper (*Psedera quinquefolia* (L.) Greene) climb trees but they do not twine around the stems so as to cause constrictions. Poison ivy climbs by means of rootlets whereas the Virginia creeper has tendrils which are usually terminated by enlarged adhesive discs.

[1] Illustrations published with the aid of the Lucien M. Underwood Memorial Fund.

The injury resulting from bittersweet is caused by the vines twining tightly around stems and branches of young trees and inhibiting, if not completely stopping, downward translocation of organic solutes. These organic substances, which are elaborated in the leaves, move downward through the tree stem in what is sometimes referred to as the "descending stream of assimilates." The pathway of this descending stream is very largely through the phloem, or more specifically, through the sieve tubes in the phloem. When normal movement of organic materials is prevented by constriction of

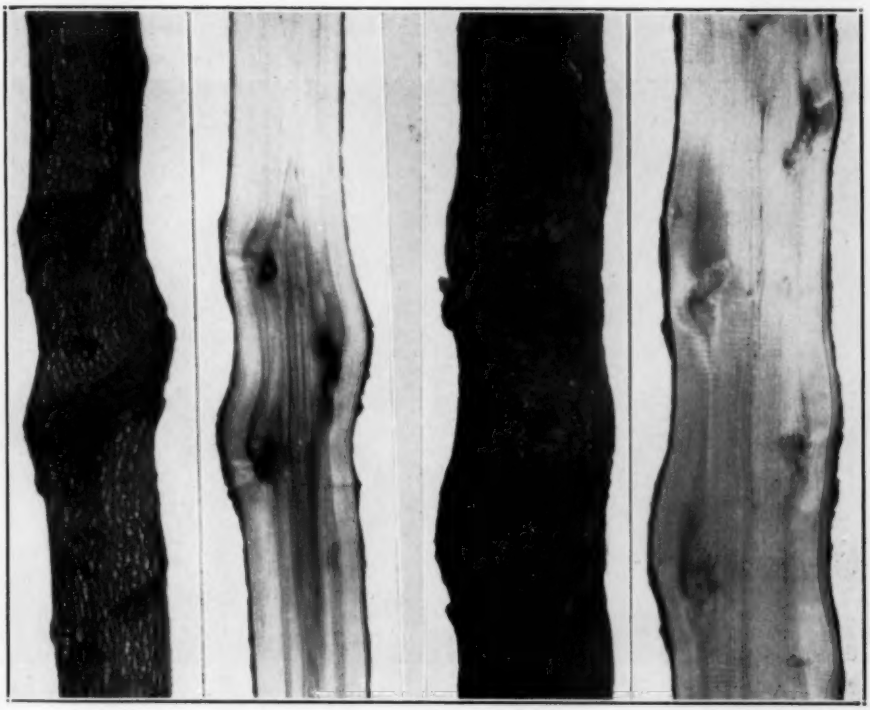

FIG. 2. Stems of *Liriodendron tulipifera* L. (left) and *Pinus strobus* L. (right) injured by bittersweet (1/10 natural size). The longitudinal sections show the character of the internal injury.

the phloem these substances accumulate in the region immediately above the point where stoppage occurred. The situation is quite analogous to that which exists when a tree stem or branch is subjected to ringing, that is, when the tissues external to the xylem are completely removed.

In twining around a tree stem the bittersweet vine takes a spiral course, the angle formed with the horizontal usually being between 50 and 70 degrees. With this relatively low pitch of the spiral, friction between the tree stem and vine stem is sufficiently great to prevent the latter from being

loosened to accommodate radial growth of the tree. Consequently, normal radial growth of the tree stem continues for only a brief period, usually one or two years, after the vine has become attached. Bittersweet is a dextrorse climber.

As a result of the damming of the descending stream, increment immediately above a constricting vine is greatly increased whereas immediately below increment is greatly lessened, or may cease. This is illustrated in figures 1 (A, B, C) and 2.[2] Trees usually are not killed by bittersweet vines because new conductive tissues are formed in which the axes of the elements are parallel to the spiral constrictions. Figure 3 illustrates this change in

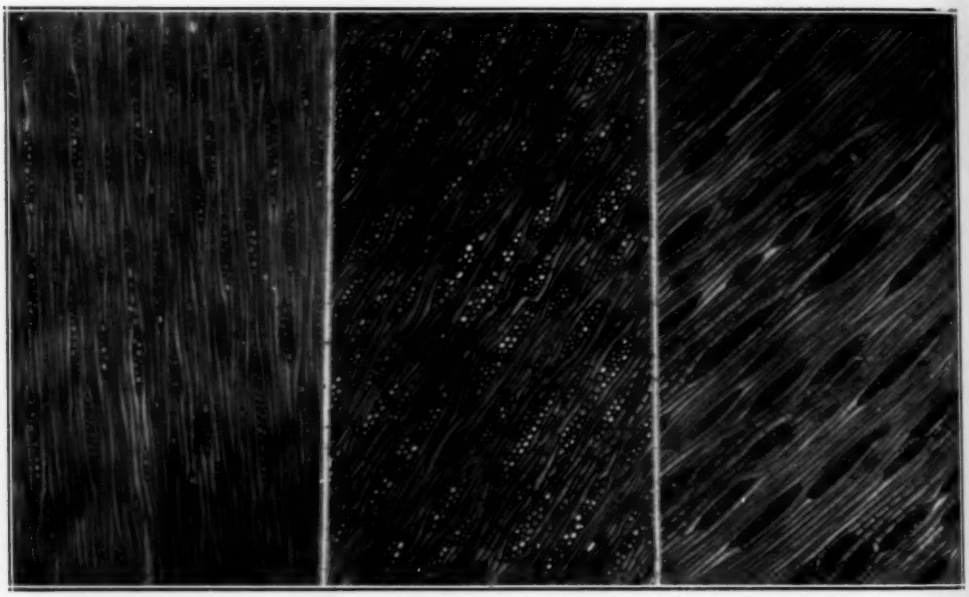

FIG. 3. Serial tangential sections showing the orientation of elements in a sassafras stem injured by bittersweet. In the section at the left, from a plane near the center of the stem, the orientation is normal. These tissues were developed before the injury. The section in the center, from a plane midway between the pith and the outside, shows the elements oriented approximately parallel to the spiral constriction. The section at the right shows an even more extreme change in orientation of elements in the outermost growth layers (×50).

orientation of elements in a sassafras stem. In stems such as those shown in figure 1 (A, B, C) the course taken by the downward moving organic solutes is a spiral.

[2] An injury similar to that caused by bittersweet is figured as the frontispiece in the April, 1942, issue of the Journal Forestière Suisse. The illustration referred to shows the effect of a honeysuckle vine on a young ash stem. It is obvious that the longitudinal section figured in the Swiss journal is upside down.

Not infrequently death of young trees has resulted from the presence of vines. With the flow of organic solutes to the roots stopped, the reserve food materials are gradually used up and the parts below the constriction die of starvation. In these cases the development of new conductive tissue was evidently so slow that the roots died before their organic food supply could be reestablished. As long as the roots remain alive upward conduction of water and inorganic solutes takes place even though the constricting vines may prevent the downward movement of organic assimilates. This is explained by the fact that the pathway of the upward moving stream is through the xylem.

Trees have been encountered which, though girdled, continued to live, in spite of the fact that downward movement of organic substances to the roots seemed impossible. It is likely that the roots of these injured trees were obtaining their organic nutrients from adjacent normal trees to which they were root-grafted. Root-grafting is evidently very common in forest trees.

In addition to the damage resulting from occlusion of bittersweet vines and bark in tree stems and the development of very abnormal wood structure, avenues are opened for entry of decay and wood borers which may render the affected trees worthless. All species of trees are subject to injury but hardwoods are more commonly damaged than conifers. The relatively dense crowns of the latter result in unfavorable light conditions for the intolerant bittersweet.

Grape vines cause a minor but interesting type of injury as a result of their tendrils coiling tightly around small tree stems and branches. Injuries of this character are illustrated in figure 1 (D to H). The tendrils cause a deformation of the tree parts analogous to that resulting from bittersweet and very frequently are occluded in the stems or branches. It is not uncommon to find a stem or branch so weakened by a tendril that it has broken off at the point of constriction.

The most serious injury from grape vines, and from other climbers such as poison ivy and the Virginia creeper, is the deformation and shading of tree crowns which they cause. Substantial damage to seedlings and middle-aged trees is commonly seen. During cultural operations in the forest it is good practice to sever the stems of all vines which are climbing trees. Exceptions may be made where the owner wishes to retain the vines as sources of food for wild life.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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(exclusive of fungi)

(See also under Morphology: **Camp & Gilly**; under Genetics: **Anderson & Hubricht, Smith**)

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